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Hispaniolan Annulariidae (Gastropoda), primarily from the Barahona Peninsula: New taxa and notes

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ABSTRACT

Eleven new taxa of Hispaniolan Annulariidae are described: *Abbottella* (*Abbottella*) *urbana* new species, *Chondropoma* (*Chondropoma*) *crystallinum* new species, *Chondropoma* (*Chondropoma*) *duffyhooksorum* new species, *Chondropoma* (*Chondropoma*) *vanattae polychroma* new subspecies, *Chondropoma* (*Wetmorepoma*) *morsecodex* new species, *Parachondria* (*Parachondria*) *gettlemani* new species, *Articulipoma rhodei* new species, *Chondropominm blaineorum* new species, *Chondropominm lynx* new species, *Chondropominm ensarcum saonaense* new subspecies, and *Licina bartschi* new species. Based on new material, *Chondropoma* (*Chondropoma*) *manielense montivagum* Bartsch, 1946, is synonymized with the nominal subspecies *Chondropoma* (*Chondropoma*) *manielense manielense* Bartsch, 1946 and *Chondropoma* (*Chondropoma*) *quisquense sculptior* Bartsch, 1946 is synonymized with the nominal subspecies *Chondropoma* (*Chondropoma*) *quisquense quisquense* Bartsch, 1946. *Chondropoma* (*Chondropominm*) *vermiculatum* sensu lato Bartsch, 1946 is moved to *Crossepoma* based on opercular features. The type locality of *Chondropoma* (*Chondropominm*) *vermiculatum sallei* Bartsch, 1946 is restricted to Cabral, Barahona Province, Dominican Republic. The type locality of *Choanopoma solutum* Pfeiffer, 1852 is restricted to the southern edge of Los Haitises Mountains, N of Majagual, ca. 12 km NW of Sabana Grande de Boyá, Monte Plata Province, Dominican Republic. The type locality of *Chondropoma louveanum* Pfeiffer, 1852 is restricted to Loma del Aguacate, Sierra Martín Gracía, Barahona Province, Dominican Republic. Distributional and habitat notes are given for additional species.

Additional keywords: Hispaniola, Dominican Republic, habitat

INTRODUCTION

Bartseh (1946) and Watters (2006) rceognized the Barahona Peninsula of the Dominiean Republic as an area of high endemism for the Annulariidae. Bartsch (1946) described 21 species of Annulariidae from the peninsula out of 67 for all of the Dominican Republie. As impressive as this seems, on closer inspection it is apparent that Bartsch's species all came from relatively few sites in the eastern half of the peninsula; the western half has never been adequately sampled or reviewed. Reeent eollections there and re-examination of older collections have revealed a wealth of previously unknown species (Watters and Duffy (2010a, 2010b), Watters (2010)), the deseription of which is eontinued here.

MATERIALS AND METHODS

Length is measured from the tip of the apex or decollated spire to the end of the outer aperture. Width is measured as the maximum dimension in a plane with the aperture perpendicular to the axis of coiling. Spiral seulpture is eounted from the suture to the inside of the umbilieus. Dimensions in eaptions refer to shell length. Shells are solute if a portion of the final whorl is detached from the previous whorl; shells are adnate if they are not detaehed. Inner apertural lips are exserted if they protrude beyond the plane of the outer lips.

Abbreviations used in the text are: BMSM, The Bailey-Matthews Shell Museum, Sanibel, Florida, USA; GTW, colleetion of the author, Columbus, Ohio, USA; NHMUK, Natural History Museum, London, UK; OSUM, Ohio State University Museum of Biological Diversity, Columbus, Ohio, USA; UF, Florida Museum of Natural History, Gainesville, Florida, USA.

SYSTEMATICS

Family Annulariidae Henderson and Bartsch, 1921
Subfamily Annulariinae Henderson and Bart1sch, 1921

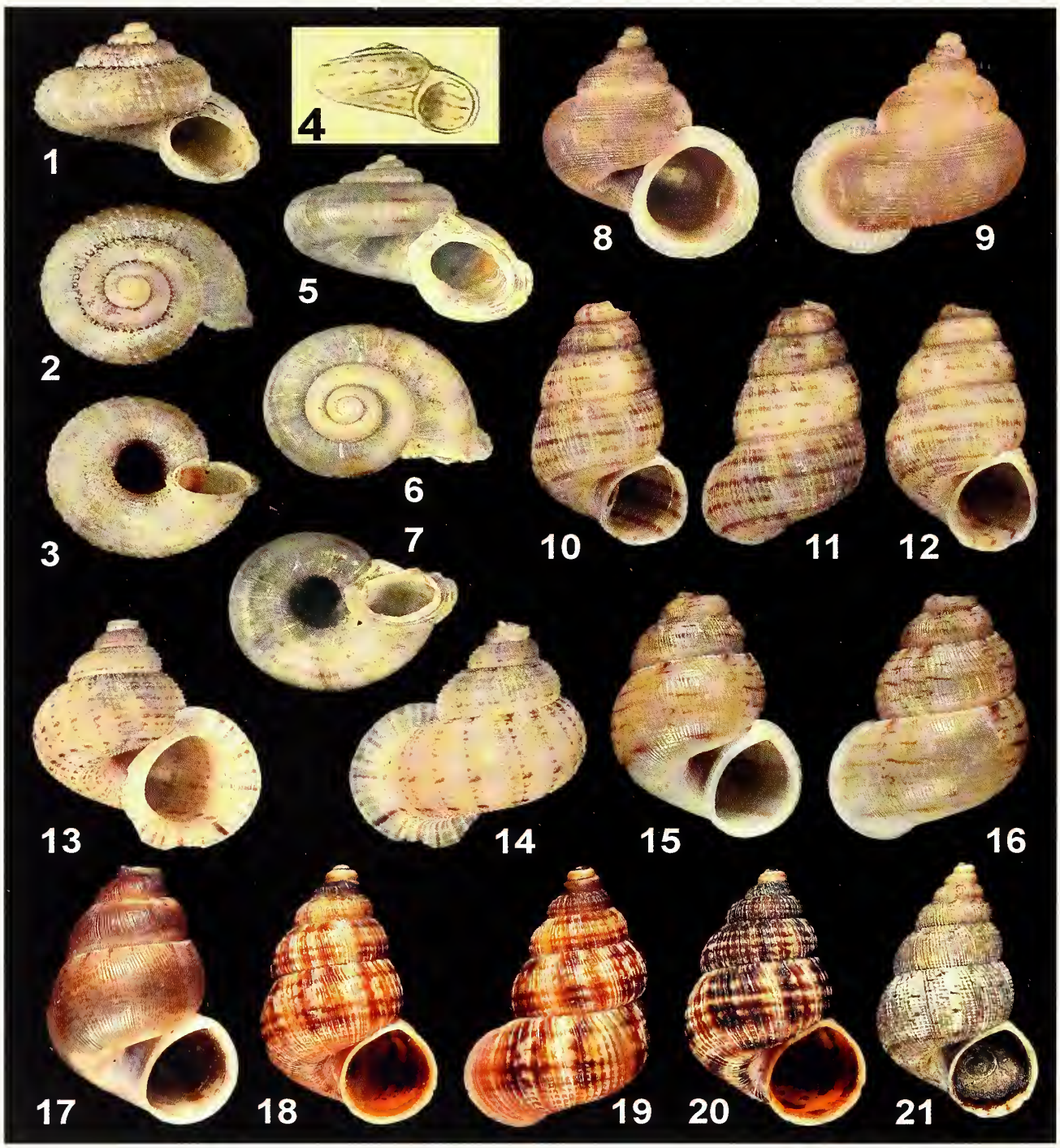
Genus *Abbottella* Henderson and Bartsch, 1921

Subgenus *Abbottella* Henderson and Bartsch, 1921

Type Species: *Chondropoma moreletianum* Crosse, 1873, by original designation.

Abbottella (Abbottella) urbana new species
(Figures 1–3)

Description (2 specimens): Shell ca. 5 mm in length, turbinoid, umbilicus wide (holotype 35% of maximum width), circular, open to apex. Nuelear whorls 1½, searcely demarcated from teleoconch, smooth, minute and erect.



Figures 1–21. *Abbottella*, *Leiabbottella*, and *Chondropoma* species. **1–3.** *Abbottella* (*Abbottella*) *urbana* new species. Holotype, UF 446061, 4.9 mm. **4–7.** *Leiabbottella soluta* (Pfeiffer, 1852). **4.** Illustration from Pfeiffer (1854b: pl. 39, fig. 8). **5–7.** UF 249105, 2 km N of Majagual, Monte Plata Province, Dominican Republic, 11.3 mm width. **8–9.** *Chondropoma* (*Chondropoma*) *crystallinum* new species. Holotype, UF 446062, 15.0 mm. **10–12.** *Chondropoma* (*Chondropoma*) *duffyhooksorum* new species. **10–11**. Holotype, UF 446063, 9.3 mm. **12**. Paratype, OSUM 36510, 8.5 mm. **13–14.** *Chondropoma* (*Chondropoma*) *manielense* Bartsch, 1946. GTW 7167b, 13 km NNE of Pedernales, Pedernales Province, Dominican Republic, 13 mm. **15–17.** *Chondropoma* (*Chondropoma*) *quisqueense* Bartsch, 1946. **15–16.** GTW 7082b, 3–4 km NW of Oviedo, Pedernales Province, Dominican Republic, 14.0 mm. **17.** GTW 7082c, 10 km NW of Oviedo on Highway 44, Pedernales Province, Dominican Republic, 13.8 mm. **18–20.** *Chondropoma* (*Chondropoma*) *vanattae polychroma* new subspecies. **18–19.** Holotype, UF 446064, 11.4 mm. **20.** Paratype, OSUM 36511, 10 km ENE of Las Mercedes, Pedernales Province, Dominican Republic, 12.2 mm. **21.** *Chondropoma* (*Chondropoma*) *vanattae vanattae* Pilsbry, 1933. GTW 7090a, Polo, Barahona Province, Dominican Republic, 13.5 mm.

Teleoconch of 3 1/4 whorls, adnate, last 1/8 whorl scarcely deflected anteriorly. Suture impressed. Peristome double, circular (holotype 1.9 mm inner peristome diameter; 2.5 mm outer peristome diameter). Outer lip thin, lamellate, evenly but narrowly expanded with a barely perceptible auricle, lip deflected abaperturally. Inner lip exserted, thick, short. Spiral sculpture of numerous, weak spiral threads (ca. 24 on final whorl), stronger and more widely spaced in umbilicus, weakest on final whorl. Axial sculpture of widely spaced threads and thicker ribs, ca. 70 on final whorl. Intersections of spiral and axial sculpture form minute pustules, somewhat stronger on spire. Axial sculpture forms weak cusps at suture. Shell dirty white with ca. 7 faint, tan narrow bands. Outer lip white with faint bands, which are apparent on both sides of lip. Operculum, anatomy, and radula unknown.

Holotype: UF 446061.

Type Locality: Parque Central, off José Contreras Blvd., N of the Loteria suburb of western Santo Domingo, Distrito Nacional, Dominican Republic, 18.44° N, –69.97° W.

Paratype: OSUM 36509, from the type locality (1 specimen).

Distribution: Lowlands just west of Santo Domingo, Dominican Republic.

Habitat: Limestone slabs.

Comparison with Other Species: Only one other species has presumably been found in the vicinity of Santo Domingo, *Abbottella moreletiana domingoensis* Bartsch, 1946. That taxon differs from *A. urbana* in its much larger adult size (ca. 12 mm diameter vs. ca. 6 mm for *A. urbana*), in having a much wider outer lip, and in having coarser sculpture (ca. 60 axial ribs vs. ca. 70 in *A. urbana*). *Abbottella urbana* is similar to *Abbottella moreletiana gabriella* Bartsch, 1946, but is even smaller (ca. 8.6 mm diameter for *A. m. gabriella*), has more numerous axial ribs (53 in *A. m. gabriella*), and has more spiral threads (ca. 24 in *A. urbana* vs. 17 in *A. m. gabriella*). Additionally, *Abbottella moreletiana gabriella* is only known from Isla San Gabriel in Samaná Bay in the easternmost part of the island.

Etymology: L. *urbanus*, of the city, in reference to the type locality of the species.

Genus ***Leiabbottella* Watters, 2010**

Type Species: *Leiabbottella galaxius* Watters, 2010, by original designation.

***Leiabbottella solutus* (Pfeiffer, 1852)**
(Figures 4–7)

Choanopoma solutum "Richard" Pfeiffer, 1852: 167.
Cyclostoma solutum (Pfeiffer, 1852). Pfeiffer, 1854b: 295, pl. 39, figs. 8–10.
Abbottella solutum (Pfeiffer, 1852). Henderson and Bartsch, 1921: 75.
Incertipoma solutum (Pfeiffer, 1852). Bartsch, 1946: 171, 173–174, pl. 30, figs. 2–4.
Rolleia? soluta (Pfeiffer, 1852). Watters, 2006: 93, 487–488.
Leiabbottella solutus (Pfeiffer, 1852). Watters, 2010: 17–18.

Distribution: Described from the "Island of Santo Domingo" Bartsch (1946) had no examples beyond Pfeiffer's description and illustration and he seemed to hint that he believed the locality was spurious. However, specimens (UF 249105) have since been collected at 150 m, southern edge of Los Haitises Mountains, N of Majagual, ca. 12 km NW of Sabana Grande de Boyá, Monte Plata Province, Dominican Republic. Specimens were collected in a coffee grove at the base of a limestone ledge in leaf mulch and under rocks (F.G. Thompson, UF, pers. comm., January, 2011). The type locality of *Choanopoma solutum* Pfeiffer, 1852 is herein restricted to 150 m, southern edge of Los Haitises Mountains, N of Majagual, ca. 12 km NW of Sabana Grande de Boyá, Monte Plata Province, Dominican Republic, 19.05° N, –69.83° W.

Subfamily Chondropomatinae Henderson and Bartsch, 1921

Genus ***Chondropoma* (*Chondropoma*) Pfeiffer, 1847**

Subgenus ***Chondropoma* Pfeiffer, 1847**

Type Species: *Cyclostoma sagra* d'Orbigny, 1842, by subsequent designation of Petit de la Saussaye, 1850.

***Chondropoma (Chondropoma) crystallinum* new species**
(Figures 8, 9)

Description (Holotype): Shell 15.0 mm maximum length, including peristome × 13.2 mm maximum width, including peristome, fragile, translucent, turbinate, umbilicus moderately wide (20% of maximum width). Protoconch whorls present in adult, 1½ whorls, not demarcated from teleoconch, smooth, minute but erect, with a diffuse brown peripheral band. Teleoconch of 4 whorls, adnate. Suture deeply impressed. Peristome double, oval (6.2 mm diameter maximum inner aperture height × 5.3 mm diameter maximum inner aperture width; 8.8 mm diameter maximum outer peristome height × 7.3 mm diameter maximum outer peristome width). Outer lip thin, expanded perpendicular to whorl, nearly evenly produced around peristome, adnate, lacking an auricle. Inner lip barely exserted, simple. Spiral sculpture present as sharp, narrow threads, weakest at periphery, ca. 39 on final whorl including umbilicus. Axial sculpture present only as numerous, minute beads on spiral threads. Suture with minute denticles. Teleoconch of faint bronze color, with 3 faint rows of narrow, widely spaced bands of darker spots at, just above, and below midline, most prominent on earlier whorls; umbilicus brown. Outer lip of peristome and portion of final whorl immediately before lip are white, unpatterned. Inner peristome bronze. Operculum, anatomy, and radula unknown.

Holotype: UF 446062.

Type Locality: 22 km N of Pedernales, off road HH to Agua Negra, at 460 m, Pedernales Province, Barahona Peninsula, Dominican Republic, in cleared field on southern slope of the Sierra de Baoruco. 18.10° N, –71.64° W.

Distribution: Known only from the type locality.

Habitat: This species was found with live and dead individuals of *Chondropoma manielense* Bartsch, 1946 and *Articulipoma rhodei* new species in a cleared field of rocks with little top soil.

Comparison with Other Species: This remarkable species is unlike any other Hispaniolan *Chondropoma*. The combination of large size, translucent shell, and nearly unicolored whorls with contrasting white peristome is unique. It is similar to *C. manielense*, with which it is found, in possessing the similar sculpture of spiral threads regularly produced into minute points; this sculpture is finer and less coarse in *C. crystallinum* than in *C. manielense*. In addition, *Chondropoma manielense* is smaller, more solid, and usually boldly patterned.

Etymology: L. *crystallinum*, of crystal, in reference to the glassy, translucent shell.

***Chondropoma (Chondropoma) duffyhooksorum* new species**
(Figures 10–12)

Description (2 specimens): Shells 8.5–9.3 mm in length (holotype 9.3 mm maximum length decollate, including peristome × 4.8 mm maximum width, including peristome), high-spired, umbilicus narrow. Protoconch whorls decollate in all examples studied. Teleoconch of 4 whorls, solute just before peristome. Suture minutely channeled. Peristome double but fused to form a single lip, tear drop-shaped (holotype 3.0 mm diameter maximum inner aperture height × 2.7 mm diameter maximum inner aperture width). Outer lip thin, not expanded except for a minute auricle. Inner lip adherent to outer lip, simple. Spiral sculpture of ca. 25 narrow, low threads, widely spaced. Axial sculpture of irregularly spaced, narrow threads (ca. 58 on final whorl), produced into minute, vertical pustules at intersections with spiral threads. Suture serrate but without cusps or tufts. Teleoconch tan with 6 darker, interrupted spiral bands equally spaced from suture through umbilicus. Operculum thin, paucispiral with a fine granular deposit. Anatomy and radula unknown.

Holotype: UF 446063.

Type Locality: On an old house, Boca Chica, at nearly sea level, Santo Domingo Province, Dominican Republic, 18.46° N, –69.61° W.

Paratype: OSUM 35610, from the type locality (1 specimen).

Distribution: Known only from the type locality.

Comparison with Other Species: *Chondropoma duffyhooksorum* is related to *Chondropoma catalinense* Bartsch, 1946 from Isla Catalina off La Romana, ca. 64 km E of Boca Chica. *Chondropoma duffyhooksorum* differs in being smaller (ca. 9 vs. ca. 12 mm in length), in the more pronounced spiral sculpture, in the nearly completely adnate final whorl (solute for 1/6th of the final whorl in *C. catalinense*), and in the better defined and continuous brown spiral bands. No similar forms have been found between Isla Catalina and Boca Chica.

The specimens also greatly resemble the crude illustrations of *Cyclostoma dominicense* Pfeiffer, 1850 given by Pfeiffer in 1854b (pl. 38, figs. 9, 10). However, Watters (2006) placed that species in *Colonina* based on examination of the syntype lot (NHMUK 1996132) and synonymized *Haitipoma catalinense* Bartsch, 1946 with it. Thus *Chondropoma catalinense* Bartsch, 1946 and *Colonina dominicense* (Pfeiffer, 1850) are both endemic to Isla Catalina and are very similar in appearance but actually belong to different genera.

Etymology: Named for Glenn Duffy and Randy Hooks, who have generously contributed many annulariid specimens for study.

***Chondropoma (Chondropoma) manielense* Bartsch, 1946**
(Figures 13, 14)

Chondropoma (Chondropoma) manielense manielense Bartsch, 1946: 53, pl. 10, fig. 3.
Chondropoma (Chondropoma) manielense montivagum Bartsch, 1946: 53, pl. 10, fig. 2.

Discussion: Bartsch (1946) described two subspecies based on differences in size and degree of coloration; both subspecies originated from the region of Manuel Viejo in the Barahona Peninsula. While variously known as Maniel Viejo to Bartsch and appearing as such on some current maps, the official name is Manuel Viejo. In the several collections reported here (GTW 7167a–d) adult specimens from the same locality range in size from 10 to 15 mm maximum length and vary from darkly colored to nearly white. There is no reason to maintain these two taxa as distinct and the subspecies *C.* (*C.*) *manielense montivagum* Bartsch, 1946 is herein synonymized with the nominal subspecies. It is curious to note that some specimens have a single peristome whereas others have a double peristome.

The records here extend the range of this species to the southern slope of the Sierra de Baoruco north of Pedernales, where it occurs under rocks in fields and in outcrops at 500–700 m. The overall range appears to be the southern slopes of the Sierra de Baoruco across the entire Barahona Peninsula.

***Chondropoma (Chondropoma) quisquense* Bartsch, 1946**
(Figures 15–17)

Chondropoma (Chondropoma) quisquense quisquense Bartsch, 1946: 61, pl. 11, fig. 1.
Chondropoma (Chondropoma) quisquense sculptior Bartsch, 1946: 61–62, pl. 11, fig. 2.

Discussion: Bartsch (1946) described C. *quisquense quisquense* from Trujin and C. *quisquense sculptior* from Manuel Viejo, both in the southeastern portion of the Barahona Peninsula. Recent collections from the Oviedo region (near Bartseh's Trujin, GTW 7082b) and Manuel Golla (15 km W of Oviedo, GTW 7082c) indieate that this species oecurs in the lowlands around the southeastern edge of the Sierra de Baorueo. Speeimens were found in fields with large hardwood trees. Bartsch differentiated the two subspeeies based on the degree to which the final whorl was solute and the strength of the sculpture. The new colleetions reported here include both subspecies within a single lot as well as intergrades. Therefore these two taxa are not eonsidered distinet and *C. (C.) quisquense sculptior* Bartsch, 1946 is herein synonymized with the nominal subspecies.

Chondropoma (Chondropoma) vanattae sensu lato Pilsbry, 1933

Chondropoma vanattae Pilsbry, 1933: 124, pl. 6, figs. 8, 9.
Chondropoma (Chondropoma) vanattae Pilsbry, 1933. Bartsch, 1946: 52, 70–71, pl. 12, fig. 3.

This speeies breaks up into three subspecies aeross the Chaîne de la Selle mountain range, from east to west: *C. vanattae vanattae* Pilsbry, 1933 in the extreme eastern part of the Sierra de Baoruco; *C. vanattae polychroma* new subspeeies on the southern slope of the western Sierra de Baoruco; and *C. vanattae verettense* Bartsch, 1946 from the Fonds-Verette region of the Massif de la Selle in Haiti.

Chondropoma (Chondropoma) vanattae polychroma new subspecies

(Figures 18–20)

Description (4 specimens): Shell 11.4–12.3 mm in length (holotype 11.4 mm maximum length, ineluding peristome × 6.8 mm maximum width, ineluding peristome), solid, eonic, umbilicus narrow (holotype 7% of maximum width). Protoconeh whorls retained in adults, 1½ whorls, scarcely demarcated from teleoconch, smooth, minute but erect, a diffuse brown band at periphery and a darker band at suture. Teleoconch of 4 whorls, solute just before peristome. Suture impressed but not channeled. Peristome single, tear drop-shaped (holotype 4.0 mm diameter maximum inner aperture height × 3.2 mm diameter maximum inner aperture width), narrow, barely expanded, lacking an auricle but posterior edge of lip forming 90° angle, inner lip just touching previous whorl. Spiral sculpture of irregularly spaced low cords of various widths, ea. 25 on final whorl, cords absent immediately below suture. Axial sculpture of irregularly spaced, wide, rounded cords of various widths with oecasional fine threads in between (ca. 70 cords on final whorl). Intersections of axial and spiral seulpture barely produced into pustules, strongest on spire. Sculpture has texture of coarse eloth. Suture serrate but lacks cusps or tufts. Teleoeonch with a light tan base with irregular dark brown blotches arranged in loose axial and spiral bands. Final 1/8th of final whorl with a pinkish hue. Inside of peristome orange. Operculum thin, paucispiral with a fine granular deposit. Anatomy and radula unknown.

Holotype: UF 446064.

Type Locality: 9 km NE of Las Mercedes, Pedernales Province, Dominican Republie, at 1000 m on trees in pine forest, 18.12° N, –71.57° W.

Paratypes: BMSM 17944 (1 specimen); OSUM 36511 (1 specimen); NHMUK 20110335 (1 specimen). All paratypes from 10 km NE of Las Mercedes, Pedernales Province, Dominican Republic, at 1300 m in pine forest, 18.13° N, –71.56° W.

Distribution: *Chondropoma vanattae polychroma* is known from 9–10 km NE of Las Mercedes at 1000–1300 m. *Chondropoma vanattae vanattae* Pilsbry, 1933 was deseribed from "Station 85, Sr. Del Monte's plantation," which was in a "verdant gully... 5–6 miles west of Barahona as the crow flies" at 1000 m. Bartsch (1946) added records from 3 km N of Manuel Viejo at 1000 m. The speeimen of *C. vanattae vanattae* illustrated here (Figure 21, GTW 7090a) is from Polo at 610 m. *Chondropoma vanattae verettense* Bartseh, 1946, was deseribed from Fonds-Verette, Haiti, at ca. 800 m. As a whole, this species occurs in the Chaîne de la Selle mountain range from ca. 600–1300 m but intergrades are not known between the subspecies.

Habitat: On trees in pine forests at ea. 1000–1300 m.

Comparison with Other Species: *Chondropoma vanattae polychroma* differs from other subspeeies of *C. vanattae* in its coarser sculpture, more vivid coloration, and in particular its orange aperture.

Etymology: Gr. *poly*, many + Gr. *chroma*, eolor, many colored, in reference to the colorful appearance of the shell.

Genus ***Chondropoma* Bartsch, 1946**

Subgenus ***Wetmorepoma* Bartsch, 1946**

Type Species: *Chondropoma (Wetmorepoma) wetmorei* Bartsch, 1946, by original designation.

Discussion: This subgenus was based on a single species, *Chondropoma wetmorei* Bartsch, 1946 from Isla Beata off the southern tip of the Barahona Peninsula. Watters and Duffy (2010a) added *C. (W.) oculeum* from the Cabo Rojo/Pedernales area of the western peninsula. A third species is deseribed here from E of Cabo Rojo westward to Oviedo. The subgenus was created by Bartsch (1946) for elongate *Chondropoma* laeking any

spiral sculpture except in the umbilicus. This subgenus appears to be a true endemic of this peninsula occurring in the lowlands of the south and west, including Isla Beata. Further genetic research will probably show *Wetmorepoma* to be a subgenus of *Chondropomium* rather than *Chondropoma*.

***Chondropoma (Wetmorepoma) morsecodex* new species**
(Figures 22, 23)

Description (21 specimens): Shells 10.0–13.0 mm in length, decollate (holotype 13.0 mm maximum length, decollate, including peristome × 6.0 mm maximum width, including peristome), translucent, high-spired, umbilicus narrow. Protoconch whorls decollate in all specimens examined. Teleoconch of 4 whorls, last $1/4^{th}$ turn free from previous whorl. Suture sharply impressed. Peristome double, tear drop-shaped (holotype 3.6 mm diameter maximum inner aperture height × 2.8 mm diameter maximum inner aperture width; holotype 4.9 mm diameter maximum outer peristome height, including auricle × 4.3 mm diameter maximum outer peristome width). Outer lip thin, expanded perpendicular to whorl, narrowest facing umbilicus, widest anterior and medial, solute from previous whorls, minute auricle present. Inner lip barely exserted, simple. Spiral sculpture present only as two very feeble cords within umbilicus. Axial sculpture of very weak, wide, low ribs, nearly obsolete on most of shell, strongest on last ¼ of final whorl. Suture smooth. Teleoconch glossy white with irregularly spaced axial bands of tan spots and dashes, four to a band; fused into a solid axial band in some specimens. Operculum paucispiral, corneous. Anatomy and radula unknown.

Holotype: UF 446065.

Type Locality: Ca. 9.3 km NW of Manuel Golla, ca. 140 m, off Highway 44, Pedernales Province, Barahona Peninsula, Dominican Republic, under rocks, 17.94° N, –71.65° W.

Paratypes: OSUM 36512 from the type locality (1 specimen); UF 249171, from 210 m, 17 km NW of Oviedo, Pedernales Province, Dominican Republic. 17.92° N, –71.51° W (15 specimens).

Other Material Examined: Jesús Santana Benítez coll., 13.5 km W of Oviedo, Pedernales Province, Dominican Republic (4 specimens).

Distribution: Lowland valley along Highway 44 from Oviedo to at least Manuel Golla, southern Barahona Peninsula.

Habitat: Specimens were found under rocks on a hill slope with limestone outcrops next to recently cleared agricultural land.

Comparison with Other Species: This is the third species described in this subgenus, all from the Barahona Peninsula. It differs from both *C. wetmorei* (Figures 24, 25) and *C. oculeum* (Figure 50) in being larger, having a wider peristome, and having a distinct pattern of dark brown rectangular spots and dashes arranged in irregularly spaced axial bands, occasionally as a single unbroken band (*C. wetmorei* has large, bold, round spots, *C. oculeum* has smaller, fainter spots).

Etymology: Morse + L. *codex*, writing, Morse code, in reference to the linear series of dots and dashes on the shell (on the holotype, from anterior to posterior, dot, dot, dot, dash = "V"). A noun in apposition.

Genus ***Parachondria* Dall, 1905**

Subgenus ***Parachondria* Dall, 1905**

Type Species: *Turbo fascia* Wood, 1828, by original designation.

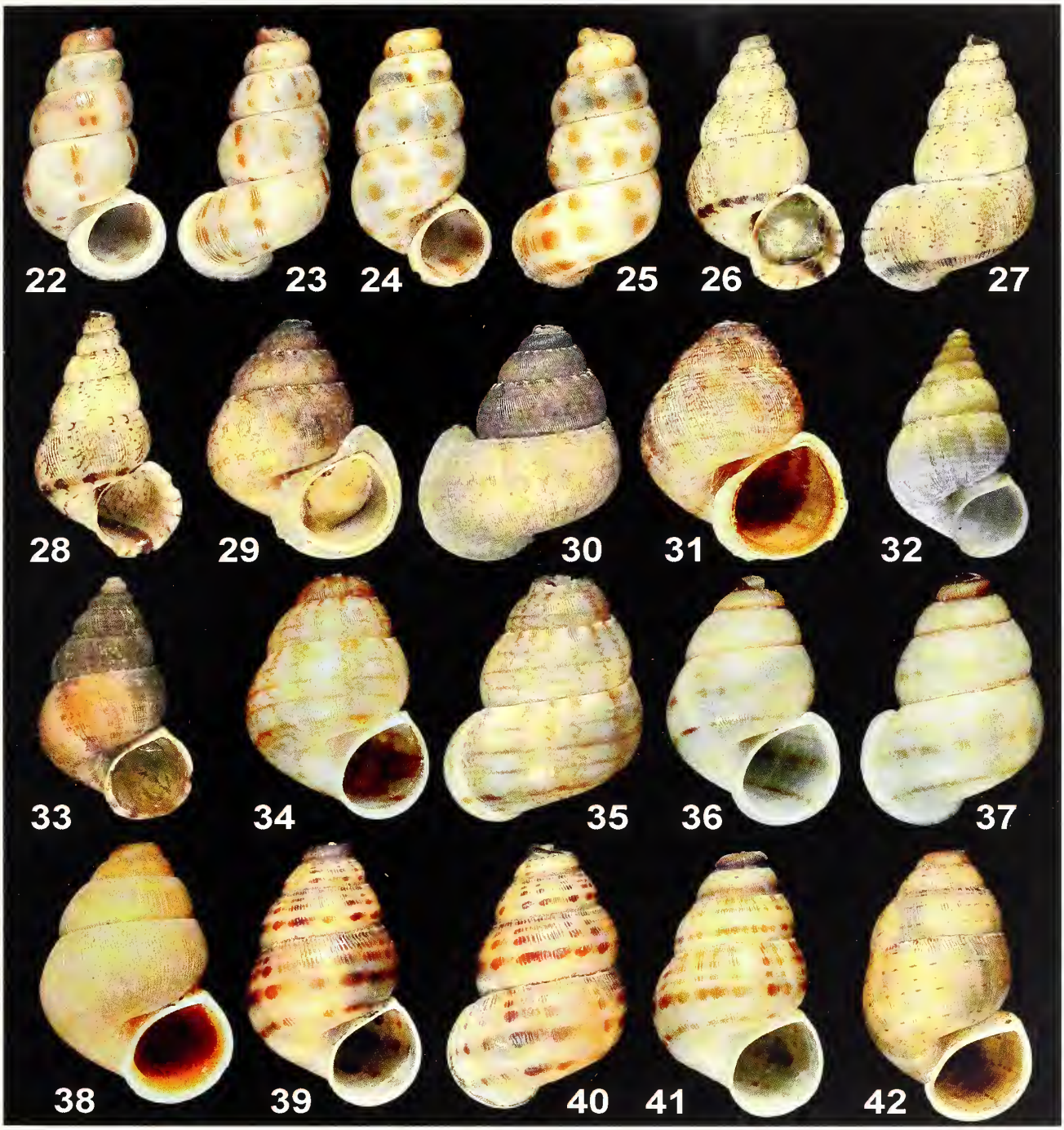
***Parachondria (Parachondria) gettlemani* new species**
(Figures 26–28, 58)

Description (7 specimens): Shell 13.9–14.6 mm in length (holotype 13.9 mm maximum length including peristome, decollate × 7.7 mm maximum width including peristome), solid, high-spired, umbilicus narrow (holotype 8% of maximum width). Protoconch whorls decollate in some adult specimens, retained in others, 1½ whorls, scarcely demarcated from teleoconch, smooth, minute but erect, white. Teleoconch of 5 whorls, adnate except for just behind peristome. Suture minutely channeled. Peristome single, tear drop-shaped (holotype 4.8 mm diameter maximum inner aperture height × 3.5 mm diameter maximum inner aperture width; holotype 6.0 mm diameter maximum outer peristome height, including auricle × 4.6 mm diameter maximum outer peristome width). Lip thin, expanded perpendicular to whorl, narrowest facing umbilicus, barely adnate to previous whorls. Small triangular auricle. Spiral sculpture present only as 2 barely perceptible cords within umbilicus. Axial sculpture of regularly spaced, narrow threads (ca. 90 on final whorl), interstices smooth. Suture broken by axial lamella as minute cusps, groups of 3–6 cusps slightly larger. Teleoconch tan with or without a pattern of small spots and fine zigzag tan markings that may coalesce to form vague, narrow bands; all specimens seen have a wide brown basal band composed of blurred, dark brown spots; there may be narrow bands between this basal band and umbilicus; wide brown band deep within umbilicus; pseudotufts white. Operculum thin, paucispiral with a granular deposit. Anatomy and radula unknown.

Holotype: UF 446066.

Type Locality: Virgen de San Rafael, ca. 200 m, ca. 7 km NNE of Paraíso, Barahona Province, Barahona Peninsula, Dominican Republic, on trees. 18.05° N, –71.12° W.

Paratypes: BMSM 17945 (1 specimen); UF 446067, juvenile (1 specimen), OSUM 36514, juveniles (2 specimens);



Figures 22–42. *Chondropoma*, *Parachondria*, *Articulipoma*, and *Chondropomium* species. **22–23.** *Chondropoma* (*Wetmorepoma*) *morsecodex* new species. Holotype, UF 446065, 13.0 mm. **24–25.** *Chondropoma* (*Wetmorepoma*) *wetmorei* Bartsch, 1946. GTW 7161a, Isla Beata, Pedernales Province, Dominican Republic, 11.3 mm. **26–28.** *Parachondria* (*Parachondria*) *gettlemani* new species. **26–27.** Holotype, UF 446066, 13.9 mm. **28.** Paratype, NHMUK 20110336, 14.3 mm, from type locality. **29–31.** *Articulipoma rhodei* new species. **29–30.** Holotype, UF 446068, 17.0 mm. **31.** Paratype, OSUM 36515, 15–20 km NE of Cabo Rojo, Pedernales Province, Dominican Republic, 14.5 mm. **32–33.** *Articulipoma lowcanum* (Pfeiffer, 1852). **32.** Syntype, NHMUK 42/10, "St. Domingo," 17 mm. **33.** UF 249153, W slope of Loma del Aguacate, Sierra Martín García, Barahona Peninsula, Dominican Republic, 14.8 mm. **34–35.** *Chondropomium blaincorum* new species. Holotype, UF 446070, 13.0 mm. **36–37.** *Chondropomium eusarcum saonaense* new subspecies. Holotype, UF 446071, 13.2 mm. **38.** *Chondropomium eusarcum catalinitense* (Bartsch, 1946). GTW 7464a, Isla Catalinita, Dominican Republic, 12.2 mm. **39–41.** *Chondropomium lynx* new species. **39–40.** Holotype, UF 446072, 19.6 mm. **41.** Paratype, OSUM 36519, Playa Los Patos, Barahona Province, Dominican Republic, 19.0 mm. **42.** *Chondropomium swiftii weinlandi* (Pfeiffer, 1862). GTW 7087c, 14 km N of Barahona, Barahona Province, Dominican Republic, 20.7 mm.

NHMUK 20110336, adult (1 specimen); all from the type locality; OSUM 36513, from 15 km S of Barahona, Barahona Province, Barahona Peninsula, Dominican Republic, on trees, 18.08° N, –71.08° W. Adult (1 specimen).

Distribution: Known only from the area from La Cienaga to Paraíso, in the narrow coastal plain between the mountains and the sea in the eastern Barahona Peninsula.

Habitat: On trees and rock fences; some specimens were found near a waterfall (Figure 58).

Comparison with Other Species: *Parachondria gettlemani* differs from *P. kazikus* (Bartsch, 1946) and *P. lindenianus* sensu lato (Weinland, 1880) in lacking any spiral sculpture outside of the umbilicus and in the presence of false tufts. *Parachondria kazikus* was described from "Dominican Republic" but has not been further localized. *Parachondria lindenianus* has a narrow range on the Massif de la Selle from Port-au-Prince to Fonds-Verette, Haiti. *Parachondria gettlemani* is only known from the area of La Cienaga, specifically Virgen de San Rafael, ca. 15 km south of Barahona, on the eastern coast of the Barahona Peninsula of the Dominican Republic.

This new species resembles members of Bartsch's (1946) *Lindenipoma*, which was synonymized with *Parachondria* by Watters (2006). This species is a good example of the reasoning behind that action. *Lindenipoma* was described by a small suite of features including the presence of spiral threads over the whorls. *Parachondria gettlemani* has all of the characteristics of *Lindenipoma* but lacks spiral sculpture except for a few cords within the umbilicus. Bartsch (1946) further noted that *Lindenipoma* lacked false tufting on the suture, which *P. gettlemani* possesses. It was this patch-work and inconsistent assortment of features that Bartsch used to delimit some of his taxa that resulted in their synonymy and inclusion into more broadly defined genera by Watters (2006).

Etymology: Named for Alan Gettleman of Merritt Island, Florida, tireless and generous collector of land snails, who collected part of the type lot.

Subfamily Tudorinae Watters, 2006

Genus ***Articulipoma* Bartsch, 1946**

Type Species: *Choudropoma* (*Articulipoma*) *caroli* Bartsch, 1946, by original designation.

Discussion: Watters (2006) raised *Articulipoma* to generic status. Species occur from the Chaîne de la Selle mountain range, including the Sierra de Baoruco in the Dominican Republic, east almost to Punta Salinas. They are characterized by axial lamellae that have an undulating or scalloped aspect. Most *Articulipoma* species are quite rare in collections.

***Articulipoma rhodei* new species**
(Figures 29–31)

Description (11 specimens): Shells 13.0–17.0 mm in length, decollate (holotype 17.0 mm maximum length, decollate, including peristome × 11.7 mm maximum width, including peristome), translucent, ovate-conic, umbilicus moderately narrow (holotype 13% of maximum width), partially covered by inner margin of outer lip. Protoconch whorls decollate in adults, 1½ whorls, scarcely demarcated from teleoconch, smooth, minute but prominent, a diffuse, brown, peripheral band may be present. Teleoconch of 4 whorls, last 1/4th turn free from previous whorl. Suture impressed and minutely channeled. Peristome double, tear drop-shaped (holotype 6.8 mm diameter maximum inner aperture height × 5.2 mm diameter maximum inner aperture width; holotype 9.8 mm diameter maximum outer peristome height, including auricle × 8.2 mm diameter maximum outer peristome width). Outer lip thin, expanded perpendicular to whorl, widest facing umbilicus, which it partially covers, solute from previous whorls in holotype but adnate in other examples. Prominent triangular auricle and wide inner portion of outer lip reflected forward, cup-like. Inner lip somewhat exserted, simple, prominent. Spiral sculpture present only as faint, wide undulations of axial threads, strongest near suture, present as 4–5 barely perceptible cords within umbilicus. Axial sculpture of regularly spaced, narrow threads (ca. 190 on final whorl), interstices smooth, having a wavy or scalloped appearance. Suture broken by axial lamella as minute cusps. Every 6–10 small cusps are followed by 3–4 enlarged but unfused cusps. Teleoconch silky in texture, bronze, purplish, tan, or orange with or without a pattern of fine zigzag tan markings that may coalesce to form bands. Suture brown with white pseudotufts. Operculum thin, paucispiral with a granular deposit. Anatomy and radula unknown.

Holotype: UF 446068.

Type Locality: 15 km NNE of Pedernales, on road to Agua Negra, Pedernales Province, Barahona Peninsula, Dominican Republic, on moist limestone cliff on the southern slope of the Sierra de Baoruco. 18.10° N, –71.64° W.

Paratypes: OSUM 36515, 15–20 km NE of Cabo Rojo, off Road HH (2 specimens), ca. 18.09° N, –71.72° W; BMSM 17946, 13 km NNE of Pedernales, on road to Agua Negra. 18.15° N, –71.70° W (2 specimens); NHMUK 20110337, 13 km NNE of Pedernales, on road to Agua Negra. 18.15° N, –71.70° W (2 specimens); UF 446069, 9.5 km NNE of Pedernales, on road to Agua Negra. 18.12° N, –71.72° W (4 specimens).

Distribution: Known from several localities on the southern slope of the Sierra de Baoruco N of Pedernales, Pedernales Province, Dominican Republic.

Habitat: Associated with limestone outerops. Speeimens have been found to ea. 1000 m. Dead speeimens have been found in cleared land adjaeent to agrieultural fields.

Comparison with Other Species: *Articulipoma rhodei* is most similar to *A. caroli* (Bartsch, 1946), but differs in being more rotund, more compaet, and generally larger (13–17 mm in length in *A. rhodei*, 11–13 mm in *A. caroli*). *Articulipoma caroli* oecurs in a narrow range on the northern side of the Massif de la Selle from Croix des Bouquets to Bodarie, Haiti. *Articulipoma rhodei* is only known from the region ca. 10–15 km north of Pedernales on the southern side of the Sierra de Baorueo, Dominiean Republie. *Articulipoma woodringi* Bartseh, 1946 differs from *A. rhodei* in lacking the pronounced auriele and in having a very narrowly expanded peristome on the inner lip (in contrast this is the widest portion in *A. rhodei*). *Articulipoma rhodei* occurs in association with *Chondropoma maneilense* Bartsch, 1946 and *Chondropoma crystallinum* new speeies.

Etymology: Named for Homer Rhode of Englewood, Florida, aecomplished eolleetor of land snails for nearly 60 years (he aceompanied sueh luminaries as Archie Jones and Edmund Winte), who collected portions of the type lot of this species.

***Articulipoma loweanum* (Pfeiffer, 1852)**
(Figure 32, 33)

Chondropoma loweanum Pfeiffer, 1852: 281.
Cyclostoma loweanum (Pfeiffer, 1852). Pfeiffer, 1854c: pl. 47, figs. 15–16.
Chondropoma (*Chondropomium*) *loweanum* Pfeiffer, 1852. Henderson and Bartsch, 1921: 60.
Chondropoma (*Articulipoma*) *loweanum* (Pfeiffer, 1852). Bartsch, 1946: 40, 48–49, pl. 8, fig. 3.
Articulipoma loweanum (Pfeiffer, 1852). Watters, 2006: 58, 337.

Distribution: Described from "Haiti," the label to the type (Figure 32, NHMUK 42/10) reads "St. Domingo." Both loealities refer to the island of Hispaniola rather than to a more speeifie place. Bartseh (1946) had no examples beyond a photo of the type. Speeimens (UF 249153) have since been colleeted on the western slope of Loma del Aguaeate at 850 m in the Sierra Martín Graeía E of the Barahona Peninsula, Barahona Province, Dominiean Republie. The type loeality of *Chondropoma loweanum* Pfeiffer, 1852 is herein restricted to Loma del Aguacate, Sierra Martín Graeía, Barahona Provinee, Dominiean Republie, ea. 19.10° N, –71.37° W.

Genus ***Chondropomium* Henderson and Bartsch, 1921**

Type Species: *Chondropoma weinlandi* Pfeiffer, 1862, by original designation.

Discussion: As more material becomes available from the Barahona Peninsula the lines between *Chondropomium* and *Chondropoma* have beeome inereasingly blurred. *Chondropomium* was ereeted for *Chondropoma* that laeked spiral seulpture outside of the umbilical region. But the suite of "*Chondropomium*"-type features that has emerged based on additional material—typically large sized with a tear drop-shaped, narrowly expanded peristome; high spire; usually unfused sutural serrations; and undulating axial sculpture—is present in species, unknown to Henderson or Bartsch, with spiral sculpture. It is clear that a reorganization of species will be neeessary in the future based on phylogenetie studies. For now it appears that *Chondropoma marmoreum* Watters and Duffy, 2010 may also be a member of *Chondropomium*. *Chondropomium hooksi* and *C. alyshae*, both Watters and Duffy (2010a), may belong to an unnamed genus, as suggested by Watters and Duffy (2010a).

***Chondropomium blaineorum* new species**
(Figures 34, 35)

Description (2 specimens): Shells ca. 13.0 mm in length, decollate (holotype 13.0 mm maximum length, decollate, ineluding peristome × 8.8 mm maximum width, ineluding peristome), solid, eonic, umbilicus rather narrow (holotype 11% of maximum width). Protoeonch whorls decollate in all specimens examined. Teleoconch of 3¼ whorls, final whorl solute for last 1/6th of whorl. Suture minutely channeled. Peristome single, tear drop-shaped (holotype, 5.1 mm diameter maximum inner aperture height × 3.5 mm diameter maximum inner aperture width). Outer lip narrow, not expanded, minute auricle present. Spiral sculpture present only as 7–8 very feeble eords within umbilicus. Axial sculpture of narrow, closely spaced, low ribs, nearly obsolete on final whorl, forming minute cusps at suture. Suture serrate. Teleoeonch base eolor pale tan with narrow darker bands having zigzag markings between them axially arranged; umbilicus and peristome white. In paratype bands are wider and markings more diffuse. Operculum, anatomy, and radula unknown.

Holotype: UF 446070.

Type Locality: ea. 9.3 km NW of Manuel Golla, ca. 140 m, off Highway 44, Pedernales Provinee, Barahona Peninsula, Dominican Republic, under rocks. 17.94° N, –71.65° W.

Paratype: OSUM 36516, from the type locality (1 specimen).

Distribution: Known only from the type locality.

Habitat: Specimens were found under rocks on a hill slope with limestone outcrops next to recently cleared agricultural land. No live-taken speeimens are known.

Etymology: Named for Matt and Dona Blaine, who helped eolleet the type lot.

Comparison with Other Species: This small species resembles *Chondropoma eusarcum* sensu lato (Pfeiffer, 1854), which on the southern coast is only known from Isla Catalinita and Isla Saona, some 300 km E of the range of *C. blaineorum*. The nominal subspecies, *C. eusacrum eusarcum*, has not been localized, but differs from *C. blaineorum* in having much coarser sculpture, particularly on the body whorl where sculpture is nearly absent in *C. blaineorum*, and in having a different color pattern.

Chondropomium eusarcum sensu lato (Pfeiffer, 1852)

Chondropoma eusarcum Pfeiffer, 1852: 281.
Cyclostoma (Chondropoma) eusarcum (Pfeiffer, 1852). Pfeiffer, 1854a: 143.
Cyclostoma eusarcum (Pfeiffer, 1852). Pfeiffer, 1854c: pl. 48, figs. 1, 2.
Chondropoma (Chondropomium) eusarcum Pfeiffer, 1852. Henderson and Bartsch, 1921: 60.
Chondropomium eusarcum (Pfeiffer, 1852). Watters, 2006: 254.

Chondropomium eusarcum saonaense new subspecies
(Figures 36, 37)

Description (2 specimens): Shells 13.2–14.1 m in length, decollate (holotype 13.2 mm maximum length, decollate, including peristome × 8.1 mm maximum width, including peristome), solid, conic, umbilicus rather narrow (holotype 13% of maximum width). Protoconch whorls decollate in all specimens examined. Teleoconch of 4 whorls, final whorl adnate. Suture minutely channeled. Peristome double but outer and inner lips fused to form a single lip, tear drop-shaped (holotype 5.5 mm diameter maximum inner aperture height × 4.0 mm diameter maximum inner aperture width). Outer lip narrowly expanded, narrowest on inner margin, small, wide auricle present. Spiral sculpture present only as 4–5 very feeble cords within umbilicus. Axial sculpture of narrow, closely spaced, low ribs, nearly obsolete on final whorl, forming minute cusps at suture. Suture serrate. Teleoconch base color glossy white with three broken spiral bands, one above, one at, and one below periphery, composed of brown rectangular spots, nearly forming a continuous band at base; peristome white with bands showing through. Operculum thin, paucispiral with a fine granular deposit. Anatomy and radula unknown.

Holotype: UF 446071.

Type Locality: Northeastern Isla Saona, Dominican Republic, ca. 18.15° N, –68.60° W.

Paratype: OSUM 36517, from the type locality (1 specimen).

Distribution: Known only from the type locality.

Habitat: Specimens were found on a limestone cliff after rain.

Comparison with Other Species: *Chondropomium eusarcum saonaense* is somewhat similar to *Chondropomium eusarcum catalinitense* (Bartsch, 1946) (Figure 38), which occurs less than 4 km away on Isla Catalinita. *Chondropomium eusarcum catalinitense* is colored a uniform pinkish brown with only the faintest trace of color bands (*C. e. saonaense* is white with obvious bands), has an orange aperture (white in *C. e. saonaense*), and has axial ribs that are much narrower and more thread-like than those of *C. e. saonaense*.

Chondropomium eusarcum is among the smallest species of the genus. If the subspecies described by Bartsch (1946) truly are conspecific then it also has one of the widest and most fragmented ranges of any Hispaniolan annulariid. The nominal subspecies was described from "Santo Domingo" and has not been localized. *Chondropomium eusarcum puertoplatense* (Bartsch, 1946) from Puerto Plata is the only *Chondropomium* known from the northern half of the island. Described from Isla Catalinita, *Chondropomium eusarcum catalinitense* is found 280 km away on the southeastern end of Hispaniola (Watters (2006) speculated that Bartsch's locality of Catalinita Island was an error for Catalina Island, however, Catalinita Island is a separate place). The subspecies described here is from Isla Saona, adjacent to Isla Catalinita. Genetic analysis may eventually determine that these four subspecies are not conspecific.

Chondropomium lynx new species
(Figures 39–41, 58)

Description (3 specimens): Shells 19.1–19.6 mm in length, decollate (holotype 19.6 mm maximum length, decollate, including peristome × 10.4 mm maximum width, including peristome), solid, high-spired conic, umbilicus rather narrow (holotype 11% of maximum width). Protoconch whorls decollate in all specimens examined. Teleoconch of 4 whorls, last 1/4th turn solute. Suture minutely channeled. Peristome single, tear drop-shaped (holotype 7.2 mm diameter maximum inner aperture height × 5.0 mm diameter maximum inner aperture width). Outer lip narrow, solute from previous whorls, minute auricle present. Spiral sculpture present only as three very feeble cords within umbilicus. Axial sculpture of wide, closely spaced, low ribs, strongest on last ¼ of final whorl, ca. 90 on final whorl, forming minute cusps at suture. Suture serrate. Teleoconch base color tan with five broken spiral bands, three above, one at, and one below periphery, composed of dark brown spots, blurred and repeated; first teleoconch whorl dark brown; peristome white. Operculum thin, paucispiral with a fine granular deposit. Anatomy and radula unknown.

Holotype: UF 446072.

Type Locality: Virgen de San Rafael, ca. 200 m, ca. 7 km NNE of Paraíso, Barahona Province, Barahona Peninsula, Dominican Republic, under rocks. 18.05° N, –71.12° W.

Paratypes: OSUM 36518, Playa Los Patos, just off Highway 44, Barahona Province, Dominican Republic, under limestone rocks. 17.96° N, –71.19° W (1 specimen); OSUM 36519, from the type locality (1 specimen).

Distribution: Known from a narrow coastal range from Virgen de San Rafael to Playa Los Patos, in the vicinity of Paraíso, Barahona Province, Dominican Republic.

Habitat: Under limestone rocks, one specimen found near a waterfall (Figure 58).

Comparison with Other Species: *Chondropomium lynx* is part of the large complex of *Chondropomium* species in the Barahona Peninsula. In its large size, sculpture, and color pattern it resembles some forms of *C. swiftii* (Figure 42). *Chondropomium swiftii* is a lowland species distributed between the Massif de la Selle to the south and the Sierra de Neiba to the north. *Chondropomium lynx* occurs to the SE in the narrow band of lowland between the ocean and the Sierra de Baoruco. It differs from *C. swiftii* in having a unique color pattern composed of spots that are overlaid and repeated slightly out of alignment. It superficially resembles *C. swiftii barahonense* (Bartsch, 1946) from ca. 25 km to the north but does not have the nearly flat-sided pupoid shape of the *C. swiftii* complex.

Etymology: *Lynx rufus*, the American bobcat or lynx; the shell has a similar color pattern. Used as a noun in apposition.

Genus ***Crossepoma* Bartsch, 1946**

Type species: Cyclostoma emilianum *Weinland, 1862, by original designation.*

***Crossepoma vermiculatum* sensu lato (Bartsch, 1946) new combination**

Discussion: For whatever reason Bartsch (1946) rarely illustrated specimens with opercula although he always included an account of the operculum in the description of the species. Bartsch must not have had any specimens with opercula of his *Chondropoma vermiculatum vermiculatum* or any of the three other subspecies as he did not mention any opercula in the descriptions. He apparently relegated the species to *Chondropoma* (*Chondropomium*) based solely on shell features, a reasonable conclusion given the shell's characteristics. But examination of live-taken material (GTW 7088b) reveals an operculum consisting of a pseudolamellum that does not completely cover the basal, corneous portion—the hallmark of *Crossepoma*. Bartsch (1946: 72) defined a pseudolamellum as a "flat plate formed by the expansion and fusion of the retractively curved opercular riblets on the outer edge." Although Bartsch (1946) considered sutural tufts a characteristic of *Crossepoma*, this feature does not occur in all taxa (i.e., *C. emilianum insulanum* Bartsch, 1946) and it does not occur in *C. vermiculatum*. These taxa (*Chondropoma* (*Chondropomium*) *vermiculatum domingense*, *C. v. nubilum*, *C. v. sallei*, and *C. v. vermiculatum*, all Bartsch, 1946) are herein allocated to *Crossepoma* Bartsch, 1946. This is the first species of *Crossepoma* to be found in the Dominican Republic. However, other Haitian species of *Crossepoma* occur in the Chaîne de la Selle mountain range, which continues into the Dominican Republic as the Sierra de Baoruco where *C. vermiculatum* is found. Other genera have the same distribution and this range extension is not unexpected.

Crossepoma vermiculatum sensu lato (Bartsch, 1946) ranges along the eastern Barahona Peninsula from Cabral south to Trujin, although two of the four subspecies were unlocalized in Bartsch's 1946 treatment. A locality for one of these two, *Crossepoma vermiculatum sallei* (Bartsch, 1946), is recorded below. This is the most eastern species of *Crossepoma*. It apparently inhabits lowlands.

***Crossepoma vermiculatum vermiculatum* (Bartsch, 1946) new combination**
(Figures 43, 57)

Chondropoma (*Chondropomium*) *vermiculatum vermiculatum* Bartsch, 1946: 29-30, pl. 3, fig. 1.
Chondropomium vermiculatum vermiculatum (Bartsch, 1946). Watters, 2006: 63, 533.

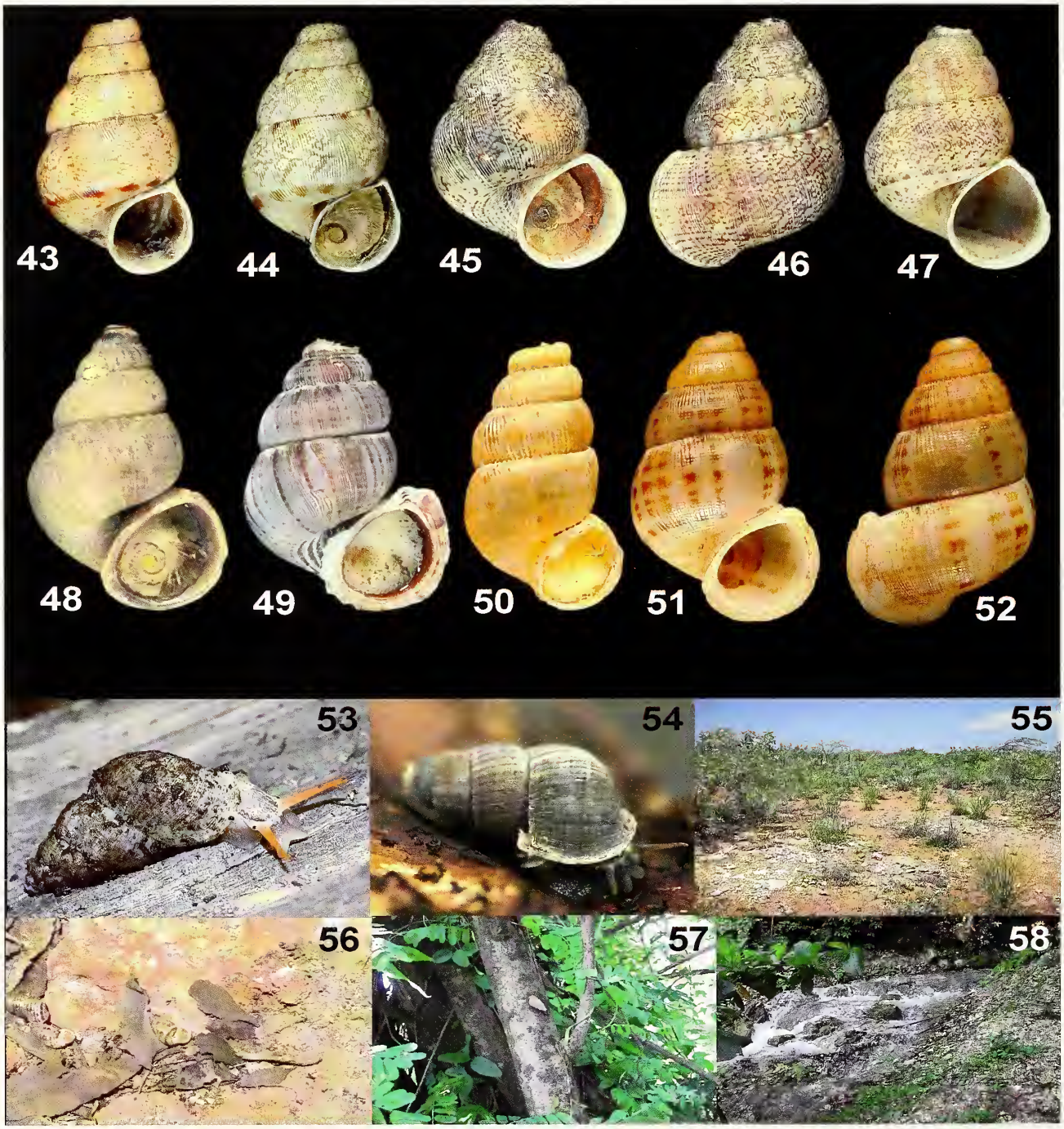
Distribution: These examples (GTW 7088b) came from the area of Colonia Juancho off Highway 44, NE of Oviedo, at 30 m along an unpaved road lined with trees, fences, and occasional rocks, 17.85° N, –71.34° W. Some individuals were found on trees (Figure 57). This area is just north of the type locality of Trujin.

***Crossepoma vermiculatum sallei* (Bartsch, 1946) new combination**
(Figure 44)

Chondropoma (*Chondropomium*) *vermiculatum sallei* Bartsch, 1946: 30, pl. 3, fig. 6.
Chondropomium vermiculatum sallei (Bartsch, 1946). Watters, 2006: 533.

Distribution: This subspecies was described from "Haiti" although Bartsch (1946) clearly did not believe that locality was correct. A specimen from Cabral (GTW 7088a), ca. 13 km WNW of Barahona, at ca. 40 m, matches the type of *C. vermiculatum sallei*. The type locality of *Chondropoma* (*Chondropomium*) *vermiculatum sallei* Bartsch, 1946 is herein restricted to Cabral, Barahona Province, Dominican Republic, ca. 18.25° N, –71.22° W. This is the northern-most subspecies.

Genus ***Licina* Gray, 1847**



Figures 43–58. *Crossepoma*, *Licina*, *Chondropomium*, and *Chondropoma* species and habitats. **43.** *Crossepoma vermiculatum vermiculatum* (Bartsch, 1946). GTW 7088b, 8 km NE of Oviedo, Pedernales Province, Dominican Republic, 15.0 mm. **44.** *Crossepoma vermiculatum sallei* (Bartsch, 1946). GTW 7088a, Cabral, Barahona Province, Dominican Republic, 18.6 mm. **45–47.** *Licina bartschi* new species. **45–46.** Holotype, UF 446073, 20.1 mm. **47.** Paratype, OSUM 36520, 20.6 mm, from type locality. **48, 53, 55.** *Chondropomium nobile* (Pfeiffer, 1852). GTW 7089b, Virgen de San Rafael, Barahona Province, Barahona Peninsula, 26.9 mm. **53.** Living animal from same locality. **55.** Habitat (photo courtesy of Alan Gettleman). **49, 54.** *Chondropomium pumilum* Watters and Duffy, 2010. GTW 7172b, 10 km NE of Las Mercedes, Pedernales Province, Dominican Republic, 19.9 mm. **54**. Living animal from same locality. **50.** *Chondropoma* (*Wetmorepoma*) *oculeum* Watters and Duffy, 2010. Holotype UF 420737, 9.0 mm. **51, 52, 56.** *Chondropoma marmoreum* Watters and Duffy, 2010. Holotype UF 420735, 18.3 mm. **56.** Habitat (photo courtesy of Alan Gettleman). **57.** Habitat of *Crossepoma vermiculatum vermiculatum* (Bartsch, 1946). Area of Colonia Juancho, NE of Oviedo, Pedernales Province, Dominican Republic (photo courtesy of Alan Gettleman). **58.** Habitat of *Parachondria gettlemani* new species and *Chondropomium lynx* new species, Virgen de San Rafael, Barahona Province, Dominican Republic (photo courtesy of Alan Gettleman).

Type Species: *Nerita labco* Müller, 1774, by original designation.

Discussion: Bartsch (1946) separated his genus *Kisslingia* from *Licina* based solely on the presence of a single peristome in the former and a double peristome in the latter. Based on the fact that among species in other genera (*Chondropoma*, for example), and occasionally even within species, taxa may have both single and double peristomes, Watters (2006) synonymized *Kisslingia* with *Licina*.

***Licina bartschi* new species**
(Figures 45–47)

Description (4 specimens): Shells 18.4–20.6 mm in length, decollate (holotype 20.1 mm maximum length, decollate, including peristome × 12.7 mm maximum width, including peristome), solid, conic, umbilicus rather narrow (holotype 12% of maximum width). Protoconch whorls decollate in adults, consisting of 1½ smooth whorls, well-delimited from teleoconch. Teleoconch of 4 whorls, final whorl solute just before peristome. Suture deeply channeled. Peristome single, thick, tear drop-shaped (holotype 7.6 mm diameter maximum inner aperture height × 5.5 mm diameter maximum inner aperture width). Outer lip narrow, barely expanded on outer side, auricle absent. Spiral sculpture present only as 3–5 very feeble cords below suture rendering axial sculpture scalloped, 7–9 cords in umbilicus. Axial sculpture of narrow, fine ribs separated by 2–3 times their width, ca. 150 on final whorl, forming minute cusps at suture. Suture serrate. Teleoconch base color glossy pale tan with a complex pattern of dense, brown, very fine, zigzag markings axially aligned, sometimes forming interrupted spiral bands on base and within umbilicus; growth rests marked by axial rows of tiny dark spots; suture with pattern of alternating white and dark brown patches; markings persist on both sides of peristome and are visible through inside of shell. Operculum paucispiral with a pseudolamella that extends 3/5ths of way to outer margin, corneous portion with a fine granular deposit. Anatomy and radula unknown.

Holotype: UF 446073.

Type Locality: 9.5 km ENE of Las Mercedes, Pedernales Province, Dominican Republic, on a mountain top at 1,300 m. 18.12° N, –71.57° W.

Paratypes: BMSM 17947, (1 specimen); OSUM 36520, (1 specimen); NHMUK 20110338, (1 specimen); all from the type locality.

Distribution: Known only from the type locality.

Habitat: In pine forest with large rock outcroppings.

Comparison with Other Species: *Licina bartschi* resembles other members of Bartsch's *Kisslingia* group (those having a simple peristome), distributed from east to west: *Licina clenchi* (Pilsbry, 1933), *Licina baharucensis* (Bartsch, 1946), *Licina polocnsis* (Bartsch, 1946), *Licina bartschi*, and *Licina hinchensis* (Bartsch, 1946). *Licina clenchi* (Pilsbry, 1933) is known only from the Barahona area and most closely resembles *L. bartschi*, even though it is the most geographically distant (50 km) of the peninsular *Kisslingia* group. *Licina bartschi* differs in being slightly larger (18–20 vs. 15–18 mm in length), having a higher spire, having more rounded whorls, and possessing thinner and more widely separated axial ribs that have a scalloped or undulating appearance over the entire body whorl. *Licina baharucensis* (Bartsch, 1946) occurs in the eastern half of the Barahona Peninsula in the Sierra de Baharuco. It is smaller, more ovate, more coarsely sculptured, and the last whorl is more solute than in *L. bartschi*. *Licina polocnsis* (Bartsch, 1946) is known only from Polo, located in a valley in east central Barahona Peninsula. It is more broadly turbinate than *L. bartschi*, with a more circular aperture (teardrop-shaped in *L. bartschi*). *Licina hinchensis* (Bartsch, 1946) is from Basin Sin (Zim) near Hinche in the Massif du Nord of central Haiti and is probably not closely related to the remaining *Kisslingia*-like taxa in the Barahona Peninsula. It is more turbinate in outline than *L. bartschi* and has a spotted rather than vermiculated color pattern. No other member of the *Kisslingia* group has such an intricate color pattern as does *L. bartschi*.

Etymology: Named for Paul Bartsch (1871–1960) of the U.S. National Museum (now National Museum of Natural History, Smithsonian Institution), who wrote the definitive works on the Annulariidae (Torre and Bartsch, 1938, 1941; Bartsch, 1946), describing nearly 800 taxa. Often vilified as a splitter, his works were nevertheless Herculean, thorough, and professional. It is surprising and disappointing that only one taxon of this family to which he devoted so much of his time (*Annularella torrebartschi* Jaume, 1984), had ever been named to honor him.

Additional Records

***Chondropoma* (*Wetmorepoma*) *oculeum* Watters and Duffy, 2010.** Originally described from 14.5 km N of Cabo Rojo, new records are from ca. 7 km S of the type locality (GTW 7166b, 7166c, Figure 50). This species seems to have a narrow range confined to the Pedernales/Cabo Rojo area on the west coast of the Barahona Peninsula.

***Chondropomium nobile* (Pfeiffer, 1852)** (Figures 48, 53, 55). One of the largest of the Annulariidae, this species was known from a few records from the coastal town of Paradis (? Paraíso), 26 km SSW of Barahona, and another record from 10 km S of Barahona. Records reported here are for Virgen de San Rafael, less than 7 km up the coast from Paraíso (GTW 7089b). Specimens were common at 200 m under rocks in dirt on

hillside erests in a scrub eactus area. It appears that this species has a very narrow range on the coastal eastern edge of the Sierra de Baorueo. A live individual is illustrated here (Figure 53).

***Chondropomium pumilum* Watters and Duffy, 2010** (Figures 49, 54). Deseribed from 19–32 km N of Cabo Rojo, new records give a more precise loeality at 10 km NE of Las Mercedes at 1,300 m in pine forests, 18.12° N, -71.56° W (GTW 7172b). It co-occurs with *Chondropoma vanattae polychroma* new subspecies.

***Chondropomium swiftii weinlandi* (Pfeiffer, 1862).** This subspeeies oeeupies a rather wide range in the xerie lowlands between the Massif de la Selle and the Sierra de Neiba, oeeurring from Thomazeau, Haiti, to Azua, Dominiean Republic. One live example was found ea. 14 km N of Barahona at the base of the Sierra de Neiba at 37 m elevation under roeks and plant roots in xerie shrub (GTW 7087e, Figure 42). Other live-taken specimens have been found at Mella (GTW 7087a) and Fordi Negro (GTW 7087b).

***Chondropoma marmoreum* Watters and Duffy, 2010.** This species is now known from several sites along the foothills of the southern Sierra de Baharuco (GTW 7170e–f). It oeeurs under rocks in xerie areas where it is locally eommon (Figures 51, 52, 56).

***Leiabbottella galaxius* Watters, 2010.** Deseribed from the Sierra de Samaná of the Samaná Peninsula, additional records extend its range westward along the north eoast to at least Sosúa, Puerto Plata Provinee (UF 249107, 249112). This is a range extension of over 100 km and illustrates how poorly the annulariid fauna of the northern eoast is known.

ACKNOWLEDGMENTS

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LITERATURE CITED

Bartsch, P. 1946. The operculate land mollusks of the family Annulariidae of the island of Hispaniola and the Bahama Archipelago. Bulletin of the U.S. National Museum 192: 264 pp., 38 pls.

Dall, W.H. 1905. An arrangement of the American Cyclostomatidae, with a revision of the nomenclature. Proceedings of Malacological Society of London 6: 208–210.

Gray, J.E. 1847. A list of the genera of Recent Mollusca, their synonyma and types. Proceedings of the Zoological Society for 1847 (15): 129–219.

Henderson, J.B. and P. Bartsch. 1921. A classification of the American operculate land mollusks of the family Annulariidae. Proceedings of the United States National Museum 58 (2327): 49–82.

Jaume, M.L. 1941. Rectificaciones a nombres de molluscos terrestres. Miscelanea Zoologica, Academia de Ciencias de Cuba (20): 1–4.

Pfeiffer, L. 1847. Uebersicht aller bekannten Arten von Cyclostomaceen. Zeitschrift für Malakozoologie 4: 101–112.

Pfeiffer, L. 1852. Monographia pneumonoporum viventum. T. Fischer, Cassellis, 435 pp.

Pfeiffer, L. 1854a. Descriptions of twenty-four new species of land shells, collected by M. Sallé on the island of St. Domingo, from Mr. Cuming's collection. Proceedings of the Zoological Society for 1852 (20): 138–144, pl. 13.

Pfeiffer, L. 1854b. Die gedeckelten Lungenschnecken. (Helicinacea et Cyclostomacea). Systematisches Conchylien-Cabinet von Martini und Chemnitz (Küster ed.). Part 19. Installment 133: pls. 37–42, pp. 269–308.

Pfeiffer, L. 1854c. Die gedeckelten Lungenschnecken. (Helicinacea et Cyclostomacea). Systematisches Conchylien-Cabinet von Martini und Chemnitz (Küster ed.). Part 19. Installment 136: pls. 43–48, pp. 309–356.

Pilsbry, H.A. 1933. Santo Domingo land mollusks collected by Samuel C. Pease, 1932, and by A. A. Olsson, 1916. Proceedings of the Academy of Natural Sciences 85: 121–162, pls. 6–11.

Watters, G.T. 2006. The Caribbean land snail family Annulariidae: a revision of the higher taxa and a catalog of the species. Backhuys Publishers, Leiden, 557 pp.

Watters, G.T. 2010. New taxa of Annulariidae from Dominican Republic (Gastropoda: Littorinoidea). Visaya 31: 16–20.

Watters, G.T. and G. Duffy. 2010a. New species of Annulariidae (Gastropoda) from the Bahamas and Dominican Republic. Novapex 11: 1–12.

Watters, G.T. and G. Duffy. 2010b. *Rolleia oberi*, new species–first record of the genus from the Dominican Republic, with a lectotype designation of *Cyclotus martensi* Maltzan, 1888 (Gastropoda: Annulariidae). The Nautilus 124: 185–187.

Americardia lightbourni new species and *A. columbella* new species compared to *A. media* (Linnaeus, 1758), *A. speciosa* (A. Adams and Reeve, 1850), and the extinct *A. columba* (Heilprin, 1886) (Bivalvia: Cardiidae)

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ABSTRACT

A comparatively small and many ribbed *Americardia* living from Bermuda, off Florida to Caribbean Panama and Brazil is described and named after J.R.H. (Jack) Lightbourn. The new species has more anterior ribs and reaches a significantly smaller size than the two other Recent western Atlantic species. It also lives in deeper water, particularly in the northern part of its distribution. It is well represented in Bermuda and Brazil but has been confounded with the much larger, lower ribbed and shallow water *Americardia media*, best known from the West Indies. A comparison of the Pliocene *Americardia columba* (Heilprin, 1886) with Recent material revealed gross similarities, yet its marked distinct rib sculpture did not allow consideration of the latter material conspecific. Thus *Americardia columbella*, living from North Carolina to Yucatan, Mexico, is also described as new herein. These two new species are compared with the type species, *A. media*, living from Florida to Ascension, and its congener *A. speciosa*, living exclusively at St. Helena. Instead of one, in Florida there are three and in Brazil two, extant *Americardia*. There is only one species living in the waters of Bermuda, North Carolina, Ascension, and St. Helena, but each of these populations represents a distinct *Americardia* species. Based on the most recent studies, the application of *Americardia* is genetically, biogeographically, and morphologically supported for this Atlantic and Eastern Pacific species complex. Consequently, *Ctenocardia* is restricted to the superficially similar but spiny Indo-Pacific species-group. According to Linnaeus, 1758 and 1767, his "O[ceano] Indico" type of *Cardium medium* should be at Uppsala only. However, no type material or trace thereof could be found there. In reality, the true identity of the Linnaean species is simply unknown and conspecificity with the Indo-Pacific *Ctenocardia fornicata* could not be excluded. To stabilize one of the "best known" Caribbean cardiids a neotype from material in the Linnean Society, London is selected, and McLean's supposed type locality, Cuba, Havana is herein confirmed.

The Natural History Museum, London [NHMUK] type material of *Cardium speciosum* is comprised of four specimens, which, however, represent two species. Only one matches the original description and is confirmed as the holotype. The other three specimens were added after 1890.

Additional keywords: Western Atlantic, Bermuda, Florida, Brazil, St. Helena, *Ctenocardia*, neotype *Cardium medium* Linnaeus, 1758, *Cardium fornicatum* G.B. Sowerby II, 1840.

INTRODUCTION

In conformity with all cardiid experts, e.g. Vidal (2000: 642), and ter Poorten (2005: 6), and most regional specialists, e.g. Clench and Smith (1944), Abbott (1974: 484), and Mikkelsen and Bieler (2008: 298), Huber (2010: 300) also recognized only one large *Americardia*, living from North Carolina to Ascension, exceptionally reaching 60 mm in the Bahamas (Redfern, 2001: 226). This species was uniformly understood as highly variable, living from shallow to rather deep water and being widely distributed, including North Carolina (Porter and Houser, 1994: 19), Bermuda (Jensen and Pearce, 2009: 344), Brazil (Rios, 2009: 1479), and Ascension (Rosewater, 1975: 33).

However, Lee (2009: 33) instead recognized *Americardia columba* from NE. Florida as valid recent species and separated it from the West Indian *A. media*. Lee further mentioned some "atypical populations" of *Americardia* from Bermuda and Brazil. Subsequently, the present authors combined their respective *Americardia* holdings resulting in nearly 30 lots with over 100 specimens collected throughout the Western Atlantic. Immediately it became obvious that not only two, but in fact three, distinct Recent species from Florida were involved. These differed in the prominence of the posterior sulcus, maximum size, number of ribs, color, and notably also in biogeography and habitat. Subsequent review of material at the Florida Museum of Natural History (FLMNH, Gainesville) by the senior author revealed 27 and 28 lots respectively of the new taxa described below. In addition, he studied 12 lots of the latter new taxon in the E.F. García Collection.

Two distinct *Americardia* species were detected in a small collection of Pliocene fossils from Florida. This led to further inquiries into that fauna, including a review of the holdings at the FLMNH. Moreover, the "well known" *Americardia* having been sorted out, the identity of Ascension Island specimens was at stake inasmuch as the obscure *Cardium speciosum* A. Adams and Reeve, 1850 recognized by E.A. Smith (1890a) as living in the

S. Atlantic, is a valid congener (Huber, 2010: Chapter 5). Thus, additionally the identity and exact distribution of *A. speciosa* had to be clarified. Moreover, the NHMUK type material contained four specimens and two species, which necessitated further inquires and solutions.

Distinction from such a well known species as *Americardia media* obviously requires an unambiguous opinion on the true identity of that Linnaeus' species. Most surprisingly, this investigation led to the fact that the London material identified by Hanley (1855) cannot represent Linnaeus' true type. In Uppsala, where, according to Linnaeus (1758 and 1767), his type should be, no specimen or traces thereof could be located. Consequently, the true identity of *Cardium medium* Linnaeus, 1758 from "Oceano Indico" is simply unknown; one could not exclude it being an earlier name for the well known Indo-Pacific *Ctenocardia fornicata*. The "firm" understanding of this "well known" American species proved neither firm nor even known, but ultimately based on mere assumptions.

As a final consideration, many modern authors use instead of *Americardia*, as proposed by Stewart (1930) and recognized by Vidal (2000), the Indo-Pacific *Ctenocardia* for this group. This is also supported by the genetic analyses performed by Kirkendale (2009).

Consequently, the authors went beyond the simple question of whether indeed a second *Americardia* lives in Florida, to investigate all Atlantic species and their generic allocation, including fossil records. A neotype for *A. media* had to be designated, the holotype for *A. speciosa* had to be identified and confirmed, and two species had to be described as new to science.

All these issues are addressed below, and two species, *Americardia lightbourni* and *Americardia columbella*, are described as new to science and compared with their two Recent Atlantic congeners.

Abbreviations used in the text are: UF: Florida Museum of Natural History, Gainesville, Florida; BMAZ: Bermuda Aquarium, Museum and Zoo, Hamilton, Bermuda; NHMUK: Natural History Museum, London; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC.

SYSTEMATICS

Family Cardiidae Lamarck, 1809
Subfamily Fraginae Stewart, 1930

Genus *Americardia* Stewart, 1930

Remarks: Type species by original designation is *Cardium medium* Linnaeus, 1758 as understood by "Reeve pl. 6 fig. 30". Stewart explicitly noted: "Should the identity of *Cardium medium* Linné with *C. medium* Reeve ever be questioned, the name *Americardia* is to go with the latter". Obviously, Stewart himself had noticeable doubts on the true identity of Linnaeus' species.

Linnaeus (1758: 678, 1767: 1122) gave O[ceano] Indico as type locality. However, this was changed early on by Gmelin (1791: 3247) to Oceano Americano. Subsequently, McLean (1939: 167) even specified Havana, Cuba. Neither of the latter authors saw or designated a type. Neither discussed or excluded the quite common, spined, white-purple Indo-Pacific *Ctenocardia fornicata* (G.B. Sowerby II, 1840). This species was unknown to Gmelin, but matches Linnaeus' original description precisely at least in context as sp. 61, in shape, in colors, in biogeography, and eventually even in sculpture "sulcis laevibus absque aculeis, angulisque obsoletis". Why should Linnaeus mention a not present feature within the very few words available? Is it indeed "without spines" or is it instead, "slightly angular ribs, smooth, where the spines are abraded"?

Linnaeus had no personal *Cardium medium* material but described this species without any references from the Swedish Queen Ulrike collection "M.L.U." (1758) and "M.L.U. 485 n. 34" (1767). It was not until later (Gmelin, 1791) that references leading to today's interpretation of the species were provided. Linnaeus based his species solely on a Swedish specimen, of which he apparently could find no satisfactory figure. Lister (1685: pl. 316, fig. 153) as proposed by Clench and Smith (1944: 21) was well known to Linnaeus, but not explicitly cited, so this lectotype designation is invalid. Linnaeus clearly excluded any type material in his personal collection (now in the Linnean Society, London) as he left no indication, which was his custom, with that material. Despite this, Hanley (1855: 47) isolated two unmarked valves in a box in Linnaeus' personal collection, though noting some differences. These, a right and a left valve, are illustrated online as *Cardium medium* <www. Linnean-online.org/16920> (Figures 18, 19). They conform well to specimens collected in Cuba and to the common understanding of *Americardia media* but definitely do not represent true Linnaean material contemporary with the description of *C. medium*. No doubt these specimens were introduced later, possibly by the son of Linnaeus or by the subsequent owner of the collection, Sir J.E. Smith.

Quite unfortunately, the Museum of Evolution, Uppsala University, could not deliver the requested species. E. Sjölin, Curator, wrote 19 October, 2010: "Regarding your request for photos of *Cardium medium* Linnaeus, 1758; I'm sorry to inform you that I couldn't find this specimen in the Museum of Evolution, or information of its whereabouts." Thus, one of the "best known" Western Atlantic cardiids has no type material; even the type locality and the true identity of *C. medium* are unsubstantiated.

To eliminate any doubts of the identity of *Cardium medium* Linnaeus, 1758, the unmarked right valve from the Linnean Society London, S.P. Dance label image G-M 0010260, well illustrated at <www.Linnean-online.org/16920/> is **selected as neotype** (Figure 19). McLean's (1939) assumed type locality, Havana, Cuba is supported. As such, *Cardium medium* Linnaeus, 1758 conforms, as anticipated by Stewart, to Reeve's interpretation and becomes the true type species of *Americardia*.

No solution other than that presented here would better serve taxonomic stability and the consistent interpretation of *C. medium* over the last 200 years. For some

time the Linnaean species was retained in *Cardium*; later it was transferred to *Fragum* (e.g. E.A. Smith, 1890a, b). Stewart (1930: 267) separated *Americardia* at the subgenus level from the New World *Trigoniocardia* and designated *Cardium medium* as its type. Stewart explicitly included the Panamic *Cardium biangulatum* Broderip and G.B. Sowerby I, 1829 but not the Caribbean *Cardium guppyi* Thiele, 1910 in *Americardia*. Stewart somewhat questioned his own subgeneric placement of *Americardia* under *Trigoniocardia* but clearly separated *Americardia* from the spiny sculptured Indo-Pacific *Ctenocardia* H. and A. Adams, 1857. In fact, narrow spined ribs are typical for the Indo-Pacific *Ctenocardia*, strongest expressed in the type species *Cardium hystrix* Reeve, 1844 non Lightfoot, 1786 (=*Cardium virgo* Reeve, 1845) weakest in *Ctenocardia gustavi* Vidal and Kirkendale, 2007. The western Atlantic *Americardia*-group, including the two well known Panamic *A. biangulata* (Broderip and G.B. Sowerby I 1829) and *A. planicostata* (Broderip and G.B. Sowerby I 1833) display broader and smoother ribs. In general, *Americardia* also grow larger and more solid than the usually smaller and more fragile Indo-Pacific *Ctenocardia*. Most conspicuous among the conchological differences is the ornamentation of the ribs: commarginal bars/knobs vs. spines respectively.

Vidal (2000) applied *Americardia* at generic level, distinct from the New World *Trigoniocardia*, and also separated from the Indo-Pacific *Ctenocardia*. Due to morphological affinities, however, Vidal placed both genera in the same group 2 within Fraginae. Ter Poorten (2005) and Mikkelsen and Bieler (2008) synonymized *Americardia* into *Ctenocardia* and combined the New World with the Indo-Pacific species. Lee (2009) and Huber (2010) did not follow those latter works, but applied *Americardia* to American species, generically distinct from the Indo-Pacific *Ctenocardia*.

Finally, Kirkendale (2009) genetically studied Fraginae. Her results are consistent with Stewart's and Vidal's view. *Americardia media* is in all clades more closely related to *Trigoniocardia* than *Ctenocardia*. Aside from disjunct biogeography and distinct morphology, the genetic data are consistent with the view here presented. The morphologically distinct "*Ctenocardia*" *victor* was recently recognized as unrelated *Freneixicardia* by ter Poorten (2009: 31). Pending further studies with additional *Ctenocardia* species and resolution of some inconsistent evidence of paraphyly among these generic units *Americardia* is herein treated as a valid genus within the cardiid subfamily Fraginae.

***Americardia lightbourni* new species**
(Figures 1–11, 21)

Diagnosis: Rather small and thin-shelled, deeper water *Americardia* with very numerous ribs, narrow interstices and a marked posterior sulcus.

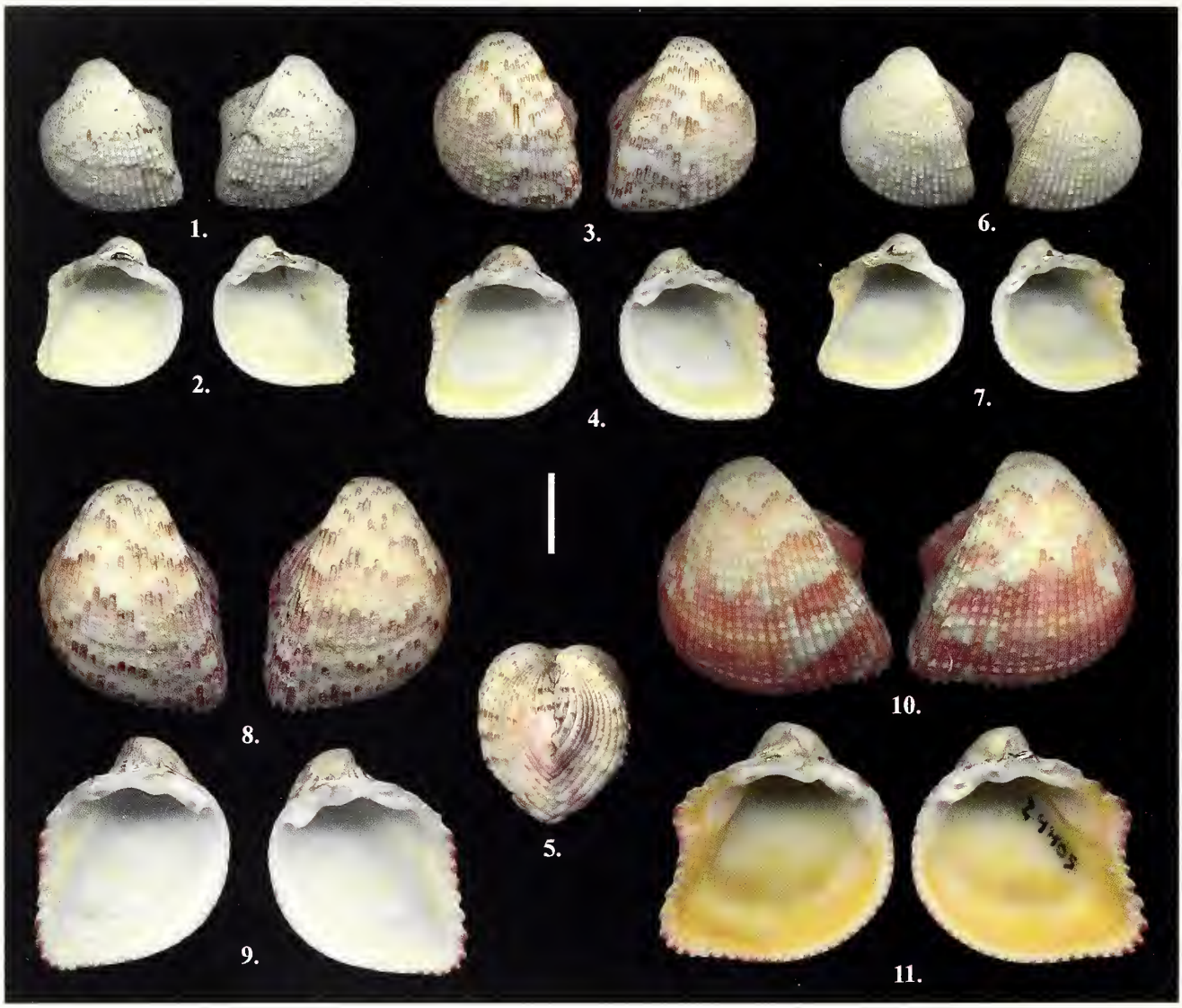
Description: Shell thin and rather fragile, inflated to strongly inflated in older specimens; moderately to strongly oblique, with a rather strong posterior sulcus. Smallest Atlantic *Americardia*, exceptionally up to 31 mm, but usually around 20 mm. Anterior margin obliquely rounded; ventral margin oblique, descending toward carina, almost imperceptibly sinuate in the posterior third. Carina sharply expressed, moderately rounded. Shell equivalve and inequilateral with rounded, weakly prosogyrous umbones placed in anterior half and extending above dorsal line. Shell surface densely radially sculptured, with 27–31, often 28 or 29, anterior ribs. Anterior ribs low, rather flat, and separated by narrow interspaces less than ¼ rib in breadth. Beneath intritacalx ribs are glossy smooth without spines, or elevated scales. Dehiscent intritacalx composed of a whitish calcareous layer, very densely and regularly commarginally lined, often forming small, irregularly arranged knobs. Ligament external, very small, dark brown, situated just posterior to umbones. External coloration whitish with irregularly arranged rose and brownish blotches and streaks. Internal shell surface porcellaneous white, usually suffused with yellow and occasionally with purplish streaks. Pallial line entire, positioned very close to the ventral margin and connecting two medium-sized, nearly homomyarian, subovate scars. Shell margin finely crenulate ventrally, but coarser on posterior margin. Hinge line strong and rather thick, with two cardinal teeth and two prominent lateral teeth. Posterior cardinal tooth in right valve and anterior lateral in left valve strong. Valves close tightly.

Variations: Size, thickness and color intensity vary remarkably within its range. Bermuda and S. Florida specimens are in general smaller with maximum sizes around 21 mm, paler and thinner, characters possibly induced by their deeper habitat. Louisiana, Caribbean Panama, and Brazilian specimens grow larger, with maximum sizes up to 32.7 mm, are often more solid, usually more brightly colored, often deep yellow inside. In the Caribbean and Brazil the species lives in much shallower water. Brazilian shells may be more elongate than the others. However, base colors and rib characters remain identical, and their habitat is still deeper than that of the type species.

Etymology: The new species name honors John (Jack) R.H. Lightbourn, who pioneered deep-water shelling in his native Bermuda and who, with the late Arthur T. Guest, discovered the holotype.

Type Locality: Bermuda Island, S. of Castle Roads, dredged in 82 m, collected by J.R.H. Lightbourn and A. T. Guest, September, 1976.

Type Material: Holotype: UF 447279, one paired specimen, 20.5 mm [Figures 1, 2], from the type locality, ex Coll. H.G. Lee. Paratype suite 1: BMAZ 2011 274 019, two paired specimens and one single right valve, 20.7 [Figures 6, 7], 20.9, and 16.3 mm respectively, from type locality, ex Coll. H.G. Lee. Paratype suite 2: Coll. M. Huber, QQ2691, one paired specimen, 25.3 mm,



Figures 1–11. *Americardia lightbourni* new species. **1–2.** Holotype Bermuda 20.5 mm. 1. External view. L, R valve. **2.** Internal view. L, R valve. **3–5.** Paratype suite 5, Brazil, 23.5 mm. **3.** External view L, R valve. **4.** Internal view, L, R valve. **5.** Posterior view, paired valves. **6–7.** Paratype suite 1, Bermuda, 20.7 mm. **6.** External view, L, R valve. **7.** Internal view L, R valve. **8–9.** Paratype suite 1, Brazil, 31.3 mm. **8.** External view, L, R valve. **9.** Internal view, L, R valve. **10–11.** Paratype suite 6, Louisiana, 32.0 mm. **10.** External view, L, R valve. **11.** Internal view L, R valve. Scale bar (all views) = 1 cm.

Caribbean Panama, off Portobello, 15 m, coral sand, dived February, 2002. Paratype suite 3: Coll. M. Huber, QQ269, one paired specimen, 21.1 mm, N. Brazil, Bahia, Alcobaça, 10–20 m, coral sand, dived March, 2005. Paratype suite 4: Coll. H.G. Lee, two paired specimens 13.1 and 15.8 mm, S. Florida, SW. Dry Tortugas, 24.736°N, 85.639°W, dredged 62.5–66.5 m, collected by E.F. García, NSF I 13. Paratype suite 5: Coll. H.G. Lee, two paired specimens, 23.5 and 31.3 mm [Figures 3, 4, 5; 8, 9 respectively], N. Brazil, Bahia, Alcobaça, 10–20 m, coral sand, dived February, 1999. Paratype suite 6: Coll. E.F. Garcia 24405, two paired specimens 21.1 and 32.0 mm [Figures 10, 11], Louisiana 28°5.85′N, 91°1.28′W, dredged 68.3 m, collected by E.F. García 3 July, 2003.

Distribution: The new species is widely distributed within the Caribbean Province, known from Bermuda, S. Florida, the Gulf of Mexico, Caribbean Panama, and Brazil. *Americardia lightbourni* is uncommon in the north but quite commonly found in Brazil.

Habitat: *Americardia lightbourni* is a sublittoral species, living from 10–100 m depth. In the southern part of its range, it is found in shallower water, 10–70 m, whereas in the north it is usually found at 50–100 m. The substrates are sand, coral-sand, and mixed carbonate rubble (off Louisiana). It is of relevance that in all collections studied the type species, *A. media,* is limited to much shallower habitats.

Discussion and Comparison: *Americardia lightbourni* can be separated from *A. media* by its higher rib number, and consequently by finer internal shell surface crenulation. The interstices are narrower, the posterior sulcus is stronger, and the valves are in general thinner and more fragile. In addition, *A. lightbourni* reaches only half the size of *A. media*. Whereas *A. media* is a common, shallow water species, often found beached, *A. lightbourni* is deeper dwelling, especially in the northern part of its distribution, and is less frequently found. The distribution of *A. lightbourni* surpasses the known range of *A. media*, which does not reach Bermuda or central Brazil.

Similarly, the new species is separated from *A. columbella* new species by its greater number of anterior ribs and a much finer crenulation of the internal margin. In addition, the area adjacent to the posterior sulcus is flat, not sunken as characteristic of *A. columbella*. The sulcus here is less marked compared to the very strong expression in *A. columbella*. *Americardia lightbourni* is more oblique compared to the rather square, upright shape of *A. columbella*. *Americardia lightbourni* is also markedly smaller and less solid than that species. Their distribution is close in Florida; otherwise *A. lightbourni* is much more widely distributed. Both species live in the sublittoral although in the northern part of its distribution *A. lightbourni* dwells in deeper water, living in general below 50 m, whereas *A. columbella* is most often found from 20 to 40 m.

From the Pliocene of Florida (e.g., APAC Pit, Sarasota) there is an apparently unnamed *Americardia* sp. (Figure 24), which has a comparable number of about 29 ribs and similar outline and surface features. Compared to Recent material, the valves of this fossil taxon are more compressed. Additionally, it is less oblique, the intercostal areas are broader, the beaks are lower and more posterior (central), and the posterior angulation is weaker. The senior author found this taxon in about ten percent of the approximately 200 Plio-Pleistocene *Americardia* lots housed at the UF collection. About half of these (approximately 10) lots also contained *A. columba*, and the two seemed to be morphologically distinct without overlap. Specimens were present in material from the Bermont, Caloosahatchee, Late Duplin, and Tamiami formations. Interestingly, only one lot referable to *A. media* was encountered [UF 35360 USA: Florida: Charlotte Co., Punta Gorda Quad, Tamiami Formation, Pinecrest Beds R. Portell! 12/23/88]. This station produced several other unusual taxa (R. Portell, pers. comm., 21 Dec., 2010). Nonetheless this extinct *Americardia* sp., apparently coeval with *A. columba* (Figure 23), may well represent the ancestor of *A. lightbourni*.

Cardium speciosum A. Adams and Reeve, 1850 was described from China in the notorious Samarang Report (see Huber, 2010: 75). As with nearly half of the bivalves newly described therein, *C. speciosum* was never again collected in Chinese waters. E.A. Smith (1890a: 302) recognized its misallocation, compared it with Atlantic specimens, and accepted it as a St. Helena species, likely collected on the return "voyage" from China.

The type material is difficult to analyze. NHMUK 74.12.11.392 represents a specimen, undoubtedly from St. Helena and labeled type. This "type" specimen is accompanied by three specimens labeled "syntypes". Thus, the whole lot contains four specimens, which, however, represent two distinct species. Originally, Adams and Reeve did not give any size or indicate more than one specimen. Furthermore, E.A. Smith (1890a: 302) only referred to "the type of this species preserved in the British Museum." Adams and Reeve clearly indicated 26 ribs. None of the present four specimens has 26 ribs. All of the three "syntypes" have far in excess of 30, up to 35 ribs. Together with shape and color, these three "syntypes" can be dismissed as subsequently introduced *A. media,* neither originating from the original lot nor St. Helena. The "type" itself has 28 ribs, two thereof admittedly rather weak. Otherwise it matches the original description well with its strongly oblique shape, moderately marked sulcus, solid texture, presence of reddish marks, and commarginally sculptured interstices. It is here recognized as the holotype (Figure 20). Consequently, the other NHMUK "syntypes" should be removed from the type collection.

In the general collection there is an unambiguous lot, NHMUK 1889.10.1.1960-4, comprised of five well preserved specimens collected in the 19th Century by Lt. W.H. Turton at St. Helena. These, together with recently collected specimens, allowed us to finally characterize *A. speciosa* as expressed herein. The exact depth of occurrence is still unknown, but it is presumed to be sublittoral.

Another lot, NHMUK 1889.10.9.38, collected by Conry at Ascension Is., is of importance. These shells confirm E.A. Smith's (1890b: 322) identification: they match *A. media* in having 25–26 anterior ribs, a solid shell, a rather broad and weakly sulcate shape, and the same color pattern. This record confirms the southernmost occurrence of this species.

In many respects *A. speciosa* and *A. lightbourni* represent extremes of this small Atlantic *Americardia*-group. *A. lightbourni* has the highest rib count; *A. speciosa* has the lowest; *A. lightbourni* is rather fragile, whereas *A. speciosa* is solid. Their maximal sizes differ markedly, and their distribution is disjunct.

Americardia columbella new species

(Figures 12–17, 22)

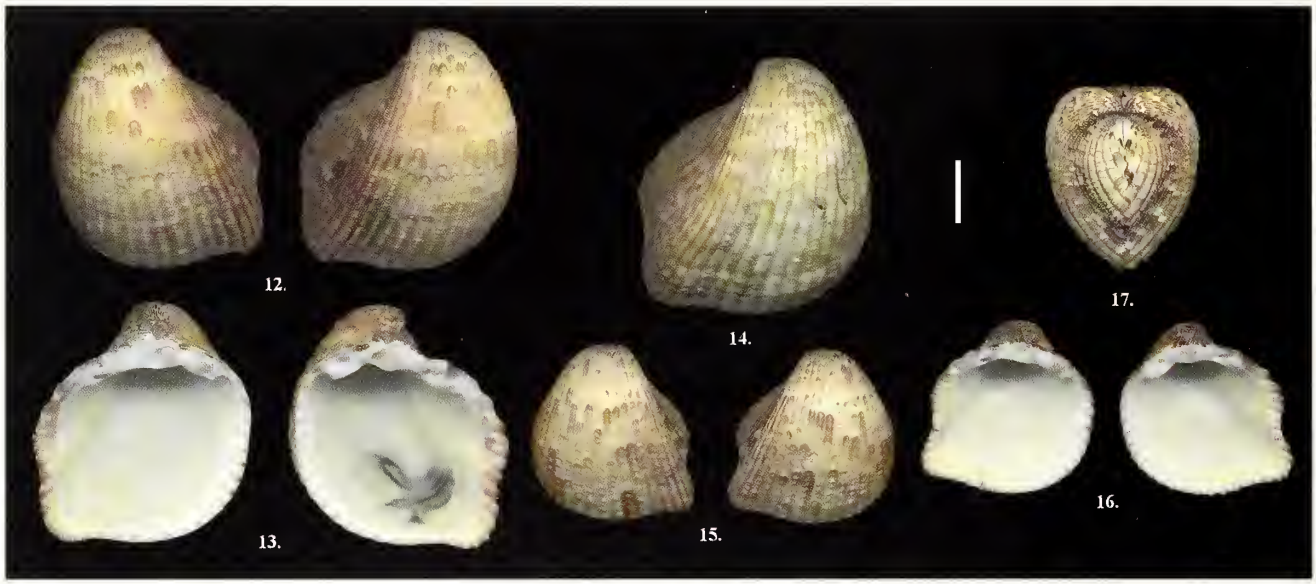
Americardia media "Linnaeus" Porter and Houser (1994: 19, North Carolina) *non* Linnaeus, 1758.

Americardia columba "Heilprin" Lee (2009: 33, pl. 7, sp. 119, NE. Florida) *non* Heilprin, 1886.

Americardia media "Linnaeus" Huber (2010: 300 fig. 11, left specimen, NE. Florida) *non* Linnaeus, 1758.

Americardia media "Linnaeus" Tunnell et al. (2010: 353, Texas) *non* Linnaeus, 1758.

Diagnosis: Large, quadrangular, orange-brown *Americardia* with distinct posterior sulcus and intermediate number of ribs, closely adjacent and without any interstices anteriorly.



Figures 12–17. *Americardia columbella* new species. **12–13.** Holotype, NE Florida, 42.2 mm **12.** External view L, R valve. **13.** Internal view L, R valve. **14.** Paratype suite 1, NE Florida, 44.5 mm. External view, R valve. **15–17.** Paratype suite 1, NE Florida, 30.1 mm. **15.** External view L, R valve. **16.** Internal view L, R valve. **17.** Posterior view, paired valves. Scale bar (all views) = 1 cm.

Description: Shell solid and thick, large for genus, reaching 44.5 mm in NE Florida, inflated to strongly inflated in old specimens; subquadrate, with a strong posterior sulcus, which is strongest extended medially. Anterior margin evenly rounded; ventral margin nearly straight, weakly sinuate in posterior third. Posterior angulation marked but moderately rounded. Shells equivalve and subequilateral, with rounded, orthogyrous umbones nearly centrally placed and clearly extending above the dorsal line. Surface radially sculptured, with 23–25, usually with 24 anterior ribs. Anterior ribs touching each other, eliminating any flat interspace as found in all other *Americardia*. Ribs subtrigonal in cross-section, with highest elevation in posterior third. Ribs beneath intritacalx glossy, smooth, without spines or elevated scales. Dehiscent intritacalx composed of orange-brown calcareous layer, very densely and regularly commarginally lined, often forming small knobs on highest part of ribs. External ligament very small, light brownish, situated just posterior to umbones. External coloration whitish with irregularly arranged orange-brown blotches and streaks. Overall shell appears brownish-orange. Internal shell surface in general glossy-white, brown along posterior margin. Pallial line entire, positioned close to ventral margin and connecting two mediums-sized, nearly homomyarian, subovate scars. Margin strongly crenulate. Crenulations broader centrally and narrower on both sides. Hinge line strong and rather thick with two cardinal teeth and two prominent lateral teeth. Posterior cardinal in right valve and anterior lateral in left valve strong. Valves close tightly.

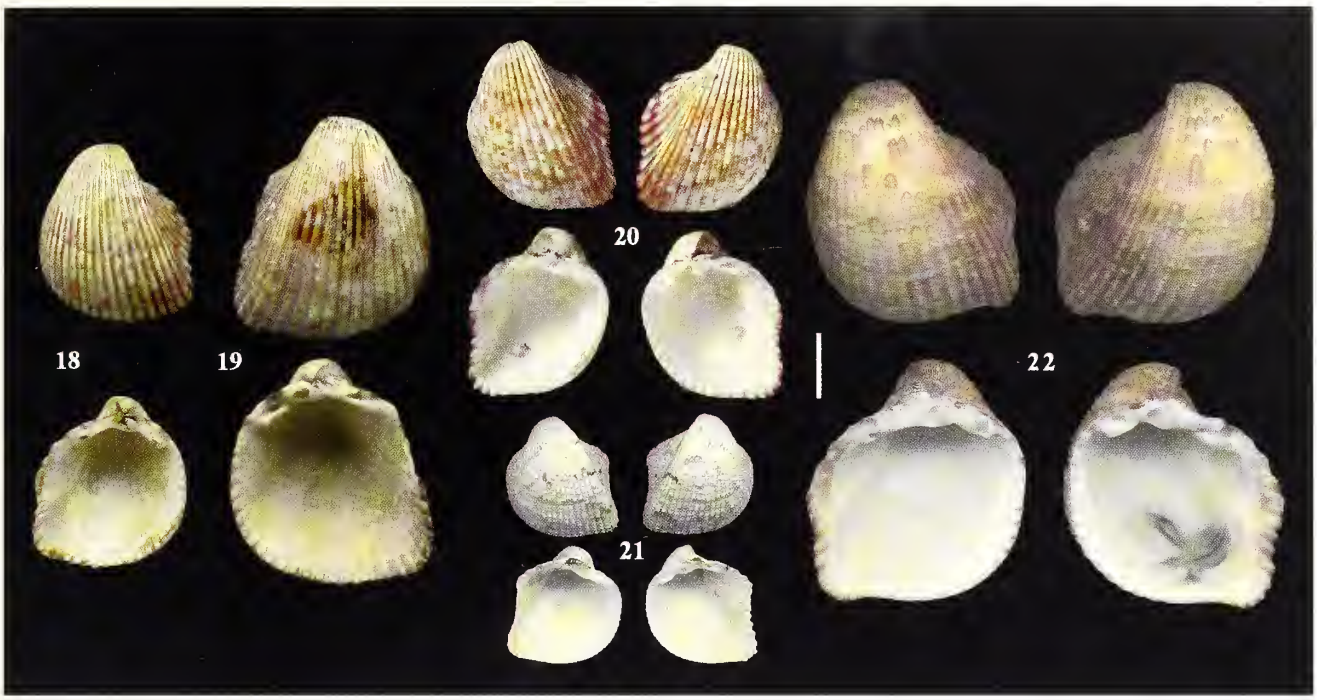
Variations: Externally, rarely a weak purplish-red band is present, in addition to the typical orange-brown blotches; inside, occasionally purplish spots or streaks are found; rarely the 3–4 ribs immediately anterior to the carina may be separated by very narrow interstices; invariably, however, the anterior portion never has interstices. In general, southern and western Florida specimens are smaller, lighter colored, and occur in deeper water.

Etymology: This new *Americardia* is named as diminutive of *columba* (from the extinct *A. columba.)* The Pliocene Florida fossil shares morphological features with and may represent the ancestor of *A. columbella.*

Type Locality: Eastern USA, NE Florida, St. Johns Co., Nine Mile Reef, 9 miles ESE St. Augustine, 22 m, near reef, on sand; 1 September, 1979, H.G. Lee (dive).

Type Material: Holotype: UF 447280, one paired specimen, 42.2 mm [Figures 12. 13], from the type locality, ex Coll. H.G. Lee. Paratype suite 1: USNM 1156949, one single valve, 44.5 mm [Figure 14], and three paired specimens, 9.9 to 30.1 mm [Figures 15, 16, 17], from the type locality, ex Coll. H.G. Lee. Paratype suite 2: Coll. M. Huber, QQ232, two paired specimens, NE. Florida, 60 miles SSE St. Augustine, dredged in 40 – 43 m, June, 1978; larger specimen, 29.2 mm illustrated in Huber (2010: 300 fig. 11, left specimen). Paratype suite 3: Coll. H.G. Lee, five paired specimens, 15.5 to 38.5 mm, same data as holotype. Paratype 4: Coll. H.G. Lee, one paired specimen, 30.6 mm; NE. Florida, Mayport, dredged in 21.5 m, November, 2009.

Distribution: This new species is narrowly restricted geographically, only known from the southeast coast of North America, from North Carolina to Yucatan. It is

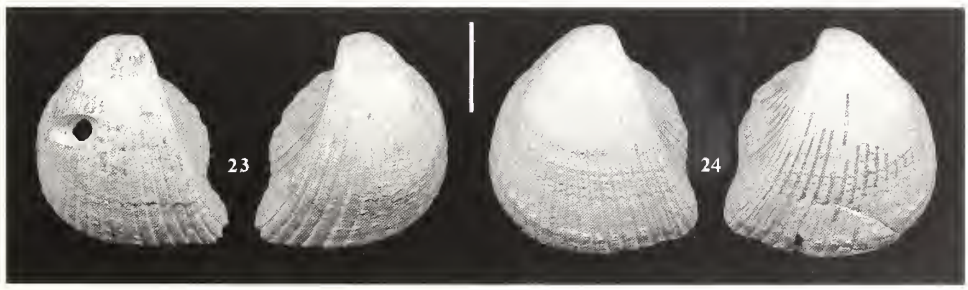


Figures 18–22. Western Atlantic *Americardia* species. **18.** *Cardium medium* Linnaeus, 1758, 29 mm, Linnean Society Collection. **19.** *Cardium medium*, neotype, Linnean Society Collection 16920 [online] (Dance image G-M 0010260), 37 mm. **20.** *Cardium speciosum* A. Adams and Reeve, 1850, holotype, NHMUK 74.12.11.392, 28.5 mm. **21.** *Americardia lightbourni*, holotype, 20.5 mm. **22.** *Americardia columbella*, holotype, 42.2 mm. Scale bar (all views) = 1 cm.

rather uncommonly encountered and rarely, if ever, cast ashore (personal observations; Andrews, 1971, 1992; Odé, 1973, 1975; Rice and Kornicker, 1962; Vokes and Vokes, 1984; UF 328133 H.E. Vokes!).

Habitat: *Americardia columbella* lives sublittorally offshore, with many records from 20–40 m, occasionally down to 60 m; the substrates vary from shell grit to coarse and fine siliceous sands, rarely on carbonate bottoms. It is of relevance that, in all collections studied, the type species, *A. media*, is restricted to much shallower habitats.

Discussion and Comparison: With the type species, *Amerieardia columbella* shares a comparatively large size, a solid shell, but also a broad hinge and an identical dentition. The rib count is comparable, although *A. media* often has one or two more anterior ribs. The carina in *A. columbella* is generally more prominent, weaker, and more rounded in *A. media*. The shape is more quadrangular upright, whereas *A. media* shape is more oblique anteriorly. *Amerieardia columbella* is most easily separated by its more prominent posterior sulcus and its more vivid orange red color. Moreover, the area adjacent to the sulcus is typically sunken in *columbella*, whereas in *A. media* this area is flat. Unmistakably distinct is the rib sculpture; *A. media* has rather flat-topped ribs with rather broad interstices, but the interstices are completely missing in *A. columbella*, and the ribs are subtrigonal in cross-section. The two



Figures 23–24. *Americardia* fossil species. **23.** *Americardia columba*, Pliocene, Florida, external view L, R valve. **24.** *Americardia* sp., Pliocene, Florida, external view L, R valve. Scale bar (all views) = 1 cm.

differ in geographic distribution: *A. media* is mainly a West Indian species, occasionally found in southern Florida and southeastern Mexico, and *A. columbella* is not known outside of eastern North America, in the Carolinian portion of the Caribbean Province. *Americardia media* lives just subtidally and is commonly beached, whereas *A. columbella* is a sublittoral species, rarely, if ever, cast ashore. The common *A. media* and the rather uncommon *A. columbella* are often found in sizes between 25–30 mm; however, the maximum size of *A. media* is 61.3 mm (West Indies, NHMUK, while *A. columbella* is not known to exceed 44.5 mm (paratype 1). *Hemicardium columba* Heilprin (1886: 93) was described as a Pliocene Floridian fossil from two left valves, illustrated on his pl. 11 figs. 26 and 26a, up to 20 mm. Heilprin compared it to the Recent *Hemicardium medium* of southern Florida. He noted 23 anterior ribs and additionally 13 on the posterior slope. Compared to *H. medium*, Heilprin noted that *H. columba* "its more upright form, the deeper hollowing of the posterior face, and the more pronounced carination of the umbonal slope". In this regard *A. columba* neatly shares the features found in the Recent *A. columbella*.

However, well preserved Pliocene fossils from Florida revealed a character not mentioned by Heilprin, namely a very distinct rib sculpture (Figure 23). In *Americardia columba*, the comparatively broad ribs are low and rather flat, separated by a deep flat channel. Thus the rib structure of *A. columba* closely approaches that of *A. media* while it is quite different from *A. columbella* with its lack of interstices and higher, subtrigonal ribs. Moreover, the Recent material is broader in shape and clearly sinuate at the margin of the valves posterior third. The original coloring of the extinct species is unknown. Due to similarities in shell shape, it is hypothesized that *A. columbella* is a comparatively young species derived from an old Floridian stock represented by *A. columba*.

Cardium speciosum is only known from St. Helena, and *A. columbella* only from the southeast coast of North America. If the locality is known, these two cannot

Table 1. Comparison of the four Recent Atlantic *Americardia* species.

	A. media	*A. lightbourni*	*A. columbella*	*A. speciosa*
anterior ribs	24–27, often 25	27–31, often 28 or 29	23–25, often 24	21–23, often 22
anterior rib sculpture	Rather flat and broad; interstices about 1/3 rib breadth	Low and narrow, rather flat, interstices less then 1/4 rib breadth	Elevated, subtrigonal, higher posteriorly, adjacent and no interstices	Subtrigonal, higher posteriorly, interstices about 1/2 rib breadth
posterior sulcus	Weakly expressed sulcus, flat adjacent area	Marked sulcus, flat adjacent area	Strongly marked sulcus, moderately to strongly hollowed adjacent area	Marked sulcus, flat adjacent area
shape	Usually moderately higher than long, weakly oblique, carina weakly expressed	Narrow (Brazil) to broadly oblique, carina sharply expressed	Quadrate, upright, carina sharply expressed	Narrow and strongly oblique, carina broadly rounded
size	61.3 mm [West Indies, NHMUK], often above 40 mm in the West Indies, but smaller in the north and in the south	Exceptionally 32.7 mm (Gulf of Mexico); 31.3 mm (Brazil), but usually smaller, not known above 21 mm in FL and Bermuda	44.5 mm (N.E. Florida), often above 30 mm in the north, smaller in the southern part of Florida	38.6 mm [NHMUK]
color	Rather uniform externally, white with brownish blotches; internally white, often marked with brownish blotches or streaks	Variable, whitish with orange, rose, and brown streaks, internally white suffused with yellow, more intensely colored in Gulf of Mexico and the south	Rather uniform, externally white with numerous orange and darker brownish blotches, internally porcelaneous white, less intensely colored in S. Florida	Rather uniform, white with numerous orange, reddish or rose blotches, internally yellowish-white, rose-red on the posterior margin
distribution	S. Florida, Bahamas, S.E. Mexico, Roatan, Puerto Rico, Venezuela, Grenada, N. Brazil, Ascension; common in the West Indies	Bermuda, S.E. Florida, Gulf of Mexico, Caribbean Panama-Central Brazil; rather common in Brazil	North Carolina to Mexico; found along entire Florida coast but uncommon in the very S., Texas, Yucatan	restricted to St. Helena
habitat	Subtidal, usually 1–13 m, up to 23 m; often beached	Sublittoral 10 – 100 m, deeper north (50–100 m), shallower south (10–70 m)	Sublittoral, 20–40 m, down to 60 m; rarely beached	unknown, presumably sublittoral

be confused. They possess a similar exterior color, reach similar sizes, and both have solid shells. However, typically their shape is markedly distinct: narrow and oblique, with a moderately expressed sulcus in *A. speciosa* and broad, subquadrangular, with a prominent sulcus in *A. columbella*. *A. speciosa* has a significantly lower rib count, with interstices of about half a rib's breadth, while in *A. columbella* the number of anterior ribs is greater, and interstices are lacking. Internally, *A. speciosa* is yellowish, even deep yellow in some specimens; *A. columbella* is glossy white within.

CONCLUSIONS

The simple question, whether the "Recent" Floridian *A. columba* is indeed distinct from "*A. media*" led to many unexpected results. Identification of material from various locations proved straightforward, with one exception. Smaller south Florida material was difficult. The cause of this predicament appears to be threefold: firstly, three species may be found there, secondly, cardiids globally develop many of their taxonomic characteristics only at medium to large size, and third, it could not be completely excluded that some specimens represent hybrids. The authors are convinced that instead of one, three species of *Americardia* live in Florida waters. A fourth Atlantic species evolved in St. Helena. Evidence suggests that a second undescribed and now extinct *Americardia* lived coevally with the well known Pliocene *A. columba* in Florida waters. Based on the diversity encountered in this study, it is suggested that *Americardia* originated in, and radiated from, this area.

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LITERATURE CITED

Abbott, R.T. 1974. American Seashells. The marine mollusca of the Atlantic and Pacific Coasts of North America. Second edition. Van Nostrand Reinhold, New York, 663 pp., 24 pls.

Adams, A. and L.A. Reeve. 1848–50. Mollusca Part 3: 45–88, pls. 18–24 (1850). In: Adams, A. (ed.), The Zoology of the voyage of H.M.S. *Samarang*; under the command of Captain Sir Edward Belcher, C.B., F.R.A.S., F.G.S. during the years 1843–1846. Reeve and Benham, London.

Andrews, J. 1971. Sea Shells of the Texas Coast. University of Texas Press, Austin, xvii + 3–298 pp.

Andrews, J. 1992. A Field Guide to Shells of the Texas Coast. Gulf Publishing Company. Houston, xxiv + 176 pp.

Clench, W.J. and L.C. Smith. 1944. The family Cardiidae in the Western Atlantic. Johnsonia 1(13): 1–31.

Gmelin, J.F. 1791. Caroli a Linné, Systema naturae, ed. 13, aucta, reformata, Vermes Testacea 1(6): 3021–3910. G. E. Beer, Lipsiae (Leipzig), Germany.

Hanley, S.C.T. 1855. Ipsa Linnaei Conchylia. The shells of Linnaeus determined from his manuscripts and collection. Williams and Norgate, London, 556 pp., 5 pls.

Heilprin, A. 1886–7. Explorations on the west coast of Florida and in the Okeechobee wilderness, with special reference to the geology and zoology of the Floridian peninsula, a narrative of researches undertaken under the auspices of the Wagner Free Institute of Science of Philadelphia. Wagner Free Institute of Science. Pp. 65–127 (1886); pp. 1–64, 128–136, pls. 1–19 (1887).

Huber, M. 2010. Compendium of Bivalves. A full-color guide to 3300 of the World's Marine Bivalves. A status on Bivalvia after 250 years of research. ConchBooks, Hackenheim, Germany, 901 pp., 1 CD.

Jensen, R.H. and T.A. Pearce. 2009. Marine Mollusks of Bermuda, checklist and bibliography. Contribution No. 13 of the Bermuda Biodiversity Project. Delaware Museum of Natural History, Greenville, 473 pp., 16 col. pls.

Kirkendale, L. 2009. Their day in the sun: molecular phylogenetics and origin of photosymbiosis in the "other" group of photosymbiotic marine bivalves (Cardiidae: Fraginae). Biological Journal of the Linnean Society 97: 448–465.

Lee, H.G. 2009. Marine shells of northeastern Florida. Jacksonville Shell Club Publication 1, (1)+204 pp, 19 pls.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tomus I. Editio duodecima, reformata. Laurentius Salvius, Holmia (Stockholm). Pp. 1–823 + i. [Reprinted in facsimile by the British Museum of Natural History, London, 1956 (+ v).]

Linné C. von. 1767. Systema Naturae, seu per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus II Editio duodecima, reformata. Laurentius Salvius, Holmia (Stockholm). Pp. 533–1327.

McLean, R.A. 1939. The Cardiidae of the Western Atlantic. Memórias de la Sociedad Cubana de Historia Natural 13(3): 157–173, pls. 23–26.

Mikkelsen, P.M. and R. Bieler. 2007. Seashells of Southern Florida—Living Marine Mollusks of the Florida Keys and Adjacent Regions: Bivalves. Princeton University Press, Princeton, 503 pp, o1500+ color illustrations.

Odé, H. 1973. A survey of the fauna of the northwest Gulf of Mexico - preliminary report (continued). Texas Conchologist 9(4): 73, 75–83.

Odé, H. 1975. Distribution and records of marine Mollusca in the northwest Gulf of Mexico (A continuing monograph) Part I - Crassatellacea - Poromyacea. Family Cardiidae. Texas Conchologist 11(4): 87–98.

Porter, H.J. and L. Houser. 1994. Seashells of North Carolina. North Carolina Sea Grant College Program, Raleigh, U.S.A. 132 pp.

Redfern, C. 2001. Bahamian Seashells: A thousand species from Abaco, Bahamas. Bahamianscahells.com Inc, Boca Raton, Florida. 280 pp. + ix, 120 pls.

Rice, W.H. and L.S. Kornicker. 1962. Mollusks of Alacran Reef, Campeche Bay, Mexico. Publications of the Institute of Marine Seience 8: 366–403.

Rios, E.C. 2009. Compendium of Brazilian Sea Shells. Femorale, Rio Grande, RS, Brazil. 676 pp.

Rosewater, J. 1975. An annotated List of the Marine Mollusks of Ascension Island, South Pacific Ocean. Smithsonian Contributions to Zoology 189: 1–41.

Smith, E.A. 1890a. Report on the marine molluscan fauna of the Island of St. Helena. Proceedings of the Zoological Society of London 1890(2): 247–317.

Smith, E.A. 1890b. Report on the marine Mollusca of Ascension Island. Proceedings of the Zoological Soeiety of London 1890(2): 317–322.

Stewart, R.B. 1930. Gabb's California Cretaceous and Tertiary type lamellibranchs. Academy of Natural Sciences Philadelphia, Special Publication 3: 3–314, 17 pls.

ter Poorten, J.J. 2005. Outline of a systematic index – Recent Cardiidae (Lamarck 1809). Visaya 16: 1–3.

ter Poorten, J.J. 2009. The Cardiidae of the Panglao Marine Biodiversity Project 2004 and the Panglao 2005 Deep-Sea Cruise with descriptions of four new species (Bivalvia). Vita Malacologica 8: 9–96.

Tunnell, J.W. Jr., J. Andrews, N.C. Barrera, and F. Moretzsohn. 2010. Encyclopedia of Texas Seashells. Texas A&M University, College Station, xi + 512 pp.

Vidal, J. 2000. Classification of Cardiidae. Phuket Marine Biological Center Special Publication 21(3): 639–644.

Vokes, H.E. and E.H. Vokes. "1983" [1984]. Distribution of shallow-water marine mollusca, Yueatan Peninsula, Mexico. Mesoamerican Ecological Institute, Monograph 1, Middle American Research Institute, Publication 54: i–viii + 1–183.

New Naticidae (Gastropoda) from Brazil

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ABSTRACT

Two new species are described from Brazil. *Notocochlis laurae* new species from the Canopus Bank, a seamount located 160 Km off Fortaleza, Ceará, is characterized by its large size, the umbilical and parietal calluses separated by a notch, a straight sulcus, and a moderately developed funicle, brownish-white color, with axial and oblique bands extending from the suture to the lower third of the whorl, and the subsutural region with a thin white spiral band. *Notocochlis isabelleana*, a shallow water species, is comparable and can be differentiated from *N. laurae* by its small size, rounded shape, coloration pattern and operculum with only one marginal rib. *Notocochlis guesti*, a deep-water species that occurs in Bermuda and the Caribbean, can be differentiated by its rounded profile, pale coloration pattern, and radular characters. *Natica jnani* new species, distributed from southern Brazil to Uruguay, has a small, smooth shell, with an obsolete funicle. Its color pattern has axial brownish zig-zag, interconnected, flammules over a white background. The internal margin of the operculum is serrate and the external margin has two thick cords. It is similar to *N. perlineata* and *N. menkeana*, both Caribbean species with different coloration pattern and a thicker funicle in the latter.

Additional keywords: Natica, Notocochlis, Canopus Bank Seamount, *Notocochlis guesti, Natica menkeana, Natica castrensis*

INTRODUCTION

About 17 species of Naticidae are known from the Brazilian coast. Except for a few rare species (e.g., *Enspira radiata* (Watson, 1881), found below 500 m) most naticid species known from this region occur in shallow waters (Rios, 1994). Nevertheless, a systematic revision of the entire family from Brazilian waters is needed. One problem in studying this family is that some genera remain inadequately defined. Many of the species are easy to identify, but some of the subfamilies and genera require better phylogenetic resolution, as some are grades, not clades. Traditionally, the genus *Natica* sensu lato has been used as a catch-all name including the numerous species belonging to the subfamily Naticinae. Pastorino (2005) recently reviewed all the species of naticids living along the Argentine coast, restricting the use of *Natica*, and using the genus *Notocochlis* Powell, 1933 for several southwestern Atlantic species hitherto placed in *Natica*.

In 2005, during a dredging expedition on the northeastern coast of Brazil, mollusks were collected between 240 and 260 m depth from Canopus Bank, off Ceará, including a new species of Naticidae, which is described in the present paper.

MATERIALS AND METHODS

Several shells and live specimens were dredged from Canopus Bank, off Ceará, Brazil, by commercial fishing boats; others are from the stomachs of the fish *Ogcocephalus vespertilio* (Linnaeus, 1758) and of the starfish *Astropecten* sp. Additionally, material from the collections of the Museu Nacional do Rio de Janeiro (MNRJ), Museu Oceanográfico Professor Eliézer de Carvalho Rios (MORG), and Museo Nacional de Historia Natural y Antropología, Montevideo (MNHNM) (collected during several cruises of the B/I Aldebarán and the R/V Academik Knipovich), were also studied.

Radulae and jaws were prepared by as in Solem (1972). Scanning Electron Microscope (SEM) photographs were taken with a Philips XL30 at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) and a JEOL JMS – 6390 LV at the Centro de Microscopia Eletrônica de Varredura at the Museu Nacional/UFRJ.

SYSTEMATICS

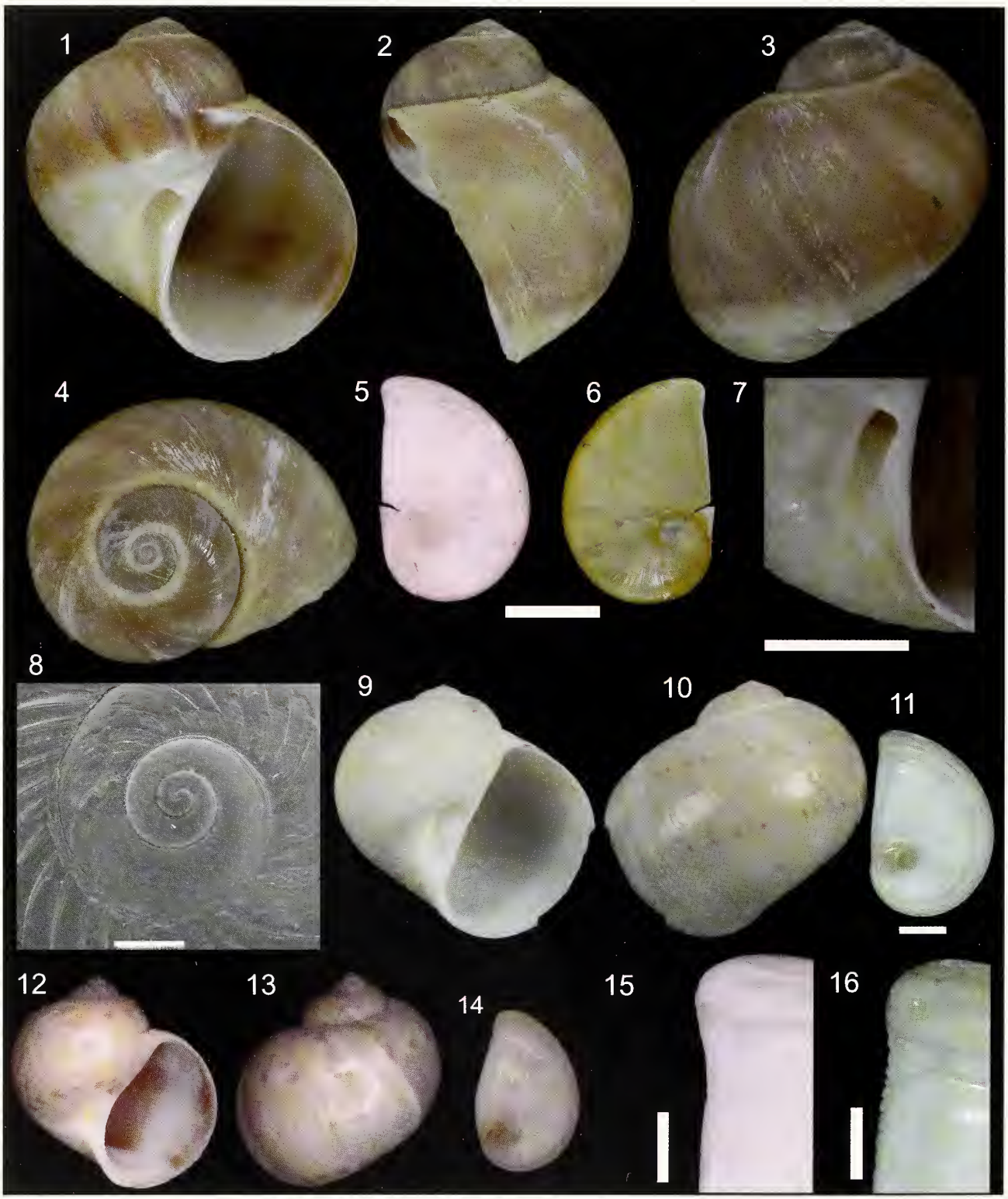
Superfamily Naticoidea Guilding, 1834
Family Naticidae Guilding, 1834
Subfamily Naticinae Guilding, 1834

Genus *Notocochlis* Powell, 1933

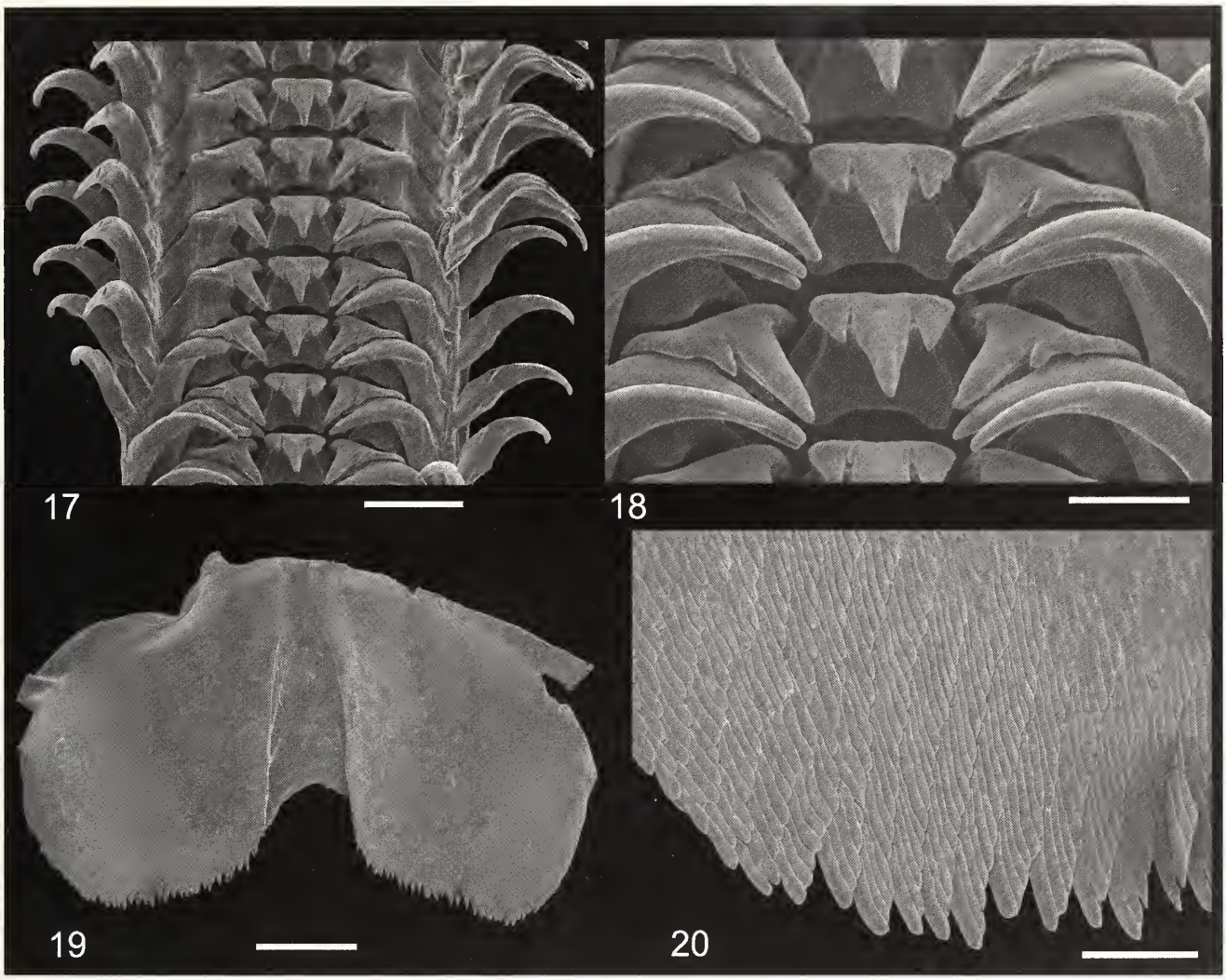
Type Species: *Cochlis migratoria* Powell, 1927, by original designation (=*N. gualteriana* Récluz, 1844).

Notocochlis laurae new species
(Figures 1–8, 15, 17–20)

Diagnosis: Shell of large size for genus, reaching about 40mm. Color brownish white, axial and oblique bands, from suture to lower third of whorl; white thin



Figures 1–16. Naticid species. **1–8, 15.** *Notocochlis laurae* new species. **1–7.** Holotype MNRJ 11866, 33.2 × 31.0 mm. **5.** External view of the operculum. **6.** Internal view of the operculum. **7.** Detail of the umbilical area. Scales bars = 1 cm. **8.** Paratype MNRJ 11867, SEM detail of the protoconch. Scale bar 500 µm. **15.** Detail of the operculum. Scale bar = 2.4 mm. **9–11, 16.** *Natica guesti* Harasewych and Jensen, 1984. **9–10.** Two views of the holotype, USNM 765087. **11.** External view of operculum. Scale bar = 1 cm. **12–14.** *Notocochlis isabelleana* MNRJ 17873, 19.5 × 18.8 mm. **12–13.** Views of shell. **14.** External view of the operculum. **16.** *Natica guesti* Harasewych and Jensen, 1984, detail of the operculum showing the smooth inner margin. Scale bar = 2.4 mm.



Figures 17–20. *Notocochlis laurae* new species. Holotype MNRJ 11866. **17.** Radulae. Scale bar = 100 μm. **18.** Detail of rachidian teeth. Scale bar = 50 μm. **19.** Jaws. Scale bar = 500 μm. **20.** Detail of the rods of the jaws. Scale bar=100 μm.

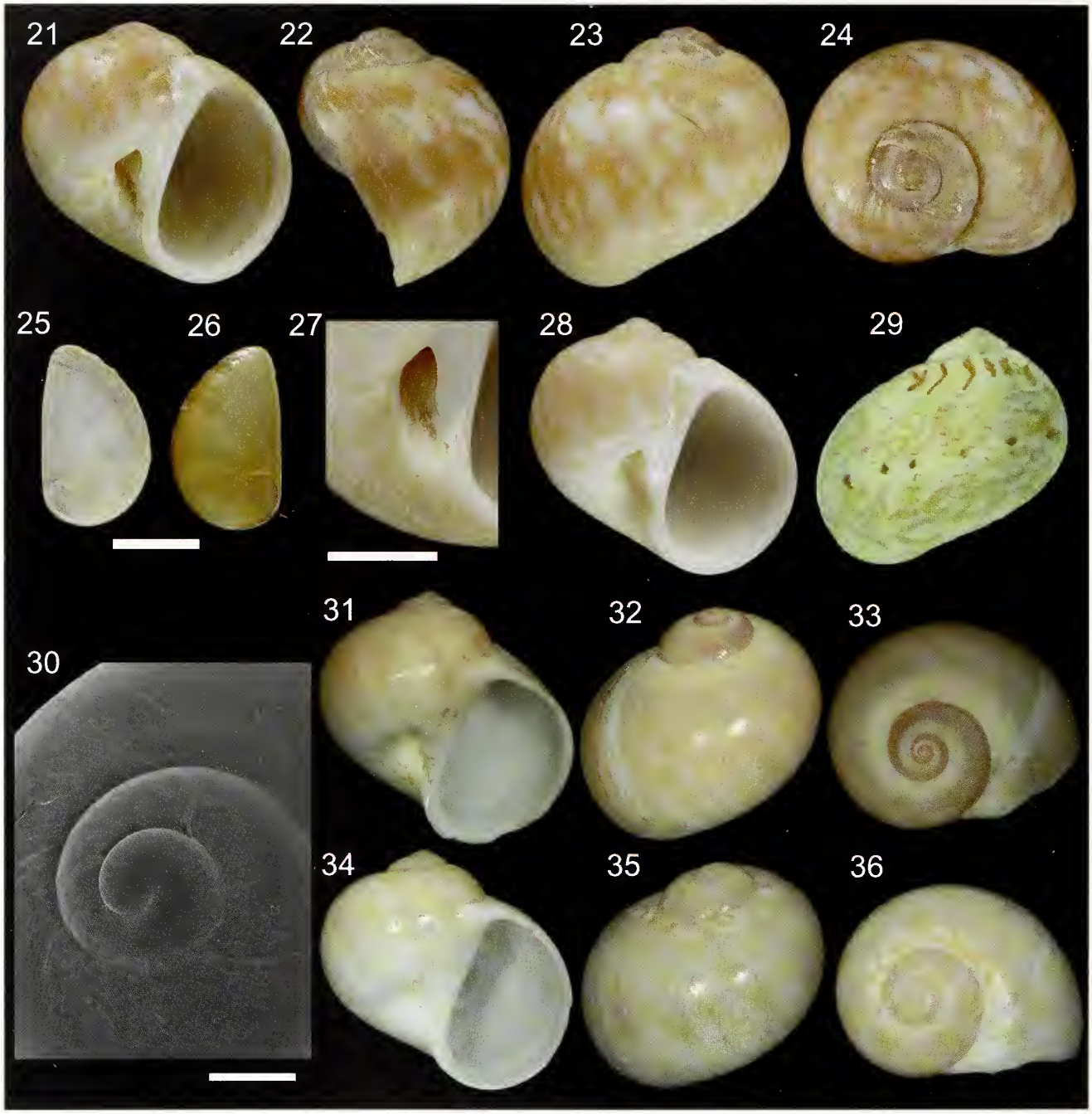
subsutural, spiral band always present. Opereulum with a smooth internal margin.

Description: Large shell (Figures 1–4, 7–8), holotype 33.2 mm in height (40.0 mm maximum height), globose, spire moderately elevated; shell thiekness average for genus; protoconch (Figure 8) of about 3.0 whorls (1.4 mm of diameter), smooth, without ornamentation, transition to teleoconch defined. Suture distinetly impressed. Teleoconch with up to three rounded whorls; axial sculpture of incised furrows on first teleoconch whorls, turning into oblique ineremental growth lines in sueeeeding whorls; suture adpressed. Parietal callus very thin, separated from umbilieal callus by notch; lobe of anterior parietal callus large, weakly defined. Umbilicus (Figure 7) moderately narrow, always open; umbilical callus moderate in size, always present; suleus deep, excavated, straight (ehannel wide, overtaking anterior internal lip without noteh); funiele moderately developed; basal lip sharp. Aperture very large, semicircular.

Color of fresh specimens brownish white, axial and oblique bands present from snture to lower third of whorl; white thin subsutural spiral band always present. Periostracum brownish, very thin.

Operculum ealeareous (Figures 5–6, 15), semicireular, solid, paueispiral, closing entire aperture. Internal opereular seulpture of growth lines, eovering whole surface; two well defined marginal ribs of angular profile, after them, a spiral groove along outer margin as wide as both marginal ribs together; caleified granulose zone on center of operculum; inner and outer margins smooth.

Radulae taenioglossate (2-1-R-1-2), rachidian teeth trapezoidal with three sharp eusps, eentral eusp larger than lateral cusps, anterior edge of base straight, posterior edge slightly convex centrally and concave at tips, ending in two sharp lateral processes. One lateral tooth

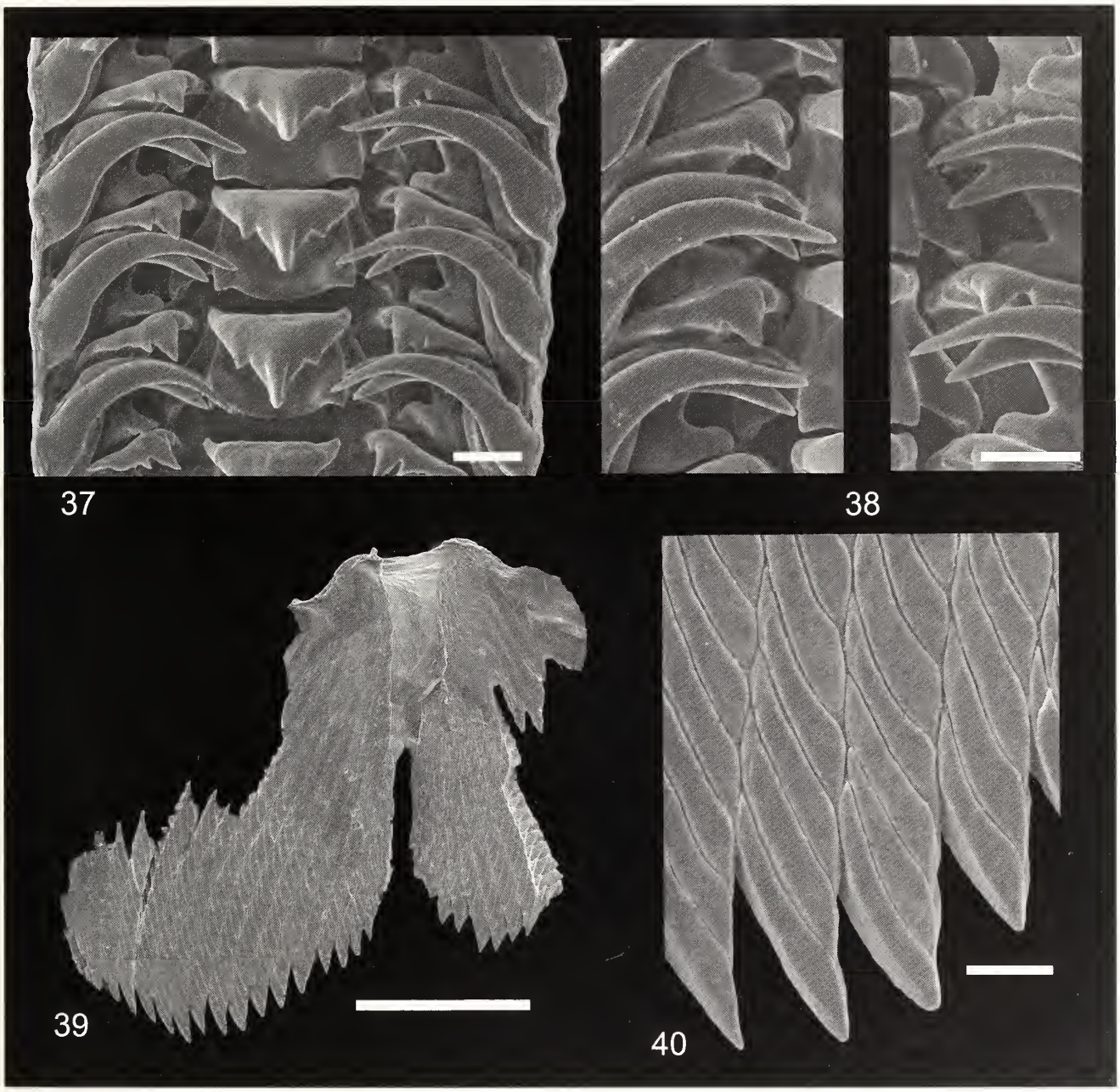


Figures 21–36. *Natica* species. **21–28, 30.** *Natica juani* new species. **21–27.** Holotype MNRJ 17876, 9.0 × 9.0 mm. **25–26.** External and internal views of the operculum scale bar = 2.5 mm. **27.** Detail of the umbilical area, scale bar = 5 mm. **28.** Paratype MNRJ 17877, 9.5 × 9.6 mm. **30.** *Natica juani* new species, Paratype MNRJ 17875, detail of the protoconch SEM picture, scale bar = 500 µm. **31–33.** *Natica perlineata*. Syntype USNM 87201, 18.0 × 18.2 mm. **34–36.** *Natica castrensis*. Syntype USNM 87198, 12.2 × 12.8 mm. **29.** *Natica menkeana*, original illustration (Philippi, 1851, pl. 15, fig. 8).

on each side, each with three cusps, central cusp four times larger than almost-obsolete lateral cusps, inner edge with two conspicuous basal prolongations. Two marginal teeth curved towards rachidian tooth; inner marginal tooth bifid with cusps of different sizes, inner cusp smaller (Figures 17–18).

Jaws trapezoidal; rods elongated, virgule shaped, diagonally arranged (Figures 19–20).

Type Material: Holotype MNRJ 11866, collected alive on 11/2005 by P. M. S. Costa and J. Coltro Jr.; Paratypes, MNRJ 11867, 12 shells and 3 opercula,



Figures 37–40. *Natica juani* new species. Holotype MNRJ 17876. **37.** Radula, frontal view, Scale bar = 20 µm. **38.** Two details of lateral teeth. Scale bar = 20 µm. **39.** Jaws. Scale bar = 200 µm. **40.** Detail of the rods of the jaws. Scale bar = 20 µm.

08/2005; MZSP 53715, 6 shells; MZSP 53926, 2 shells; MZSP 55525, 1 specimen; MZSP 70293, 7 shells; MZSP 71794, 4 shells; all paratypes from the type locality.

Type Locality: Canopus Bank, off Fortaleza, Ceará, Brazil, 02°14′25″ S, 38°22′50″ W, dredged between 240–260 m depth, from biogenic substratum, collected by P.M.S. Costa and J. Coltro Jr.

Distribution: Known from the type locality only (see map Figure 41).

Etymology: Dedicated to Laura Gomes Costa, daughter of the senior author.

Remarks: The new species has the diagnostic characters of the genus *Notocochlis*, an operculum with two

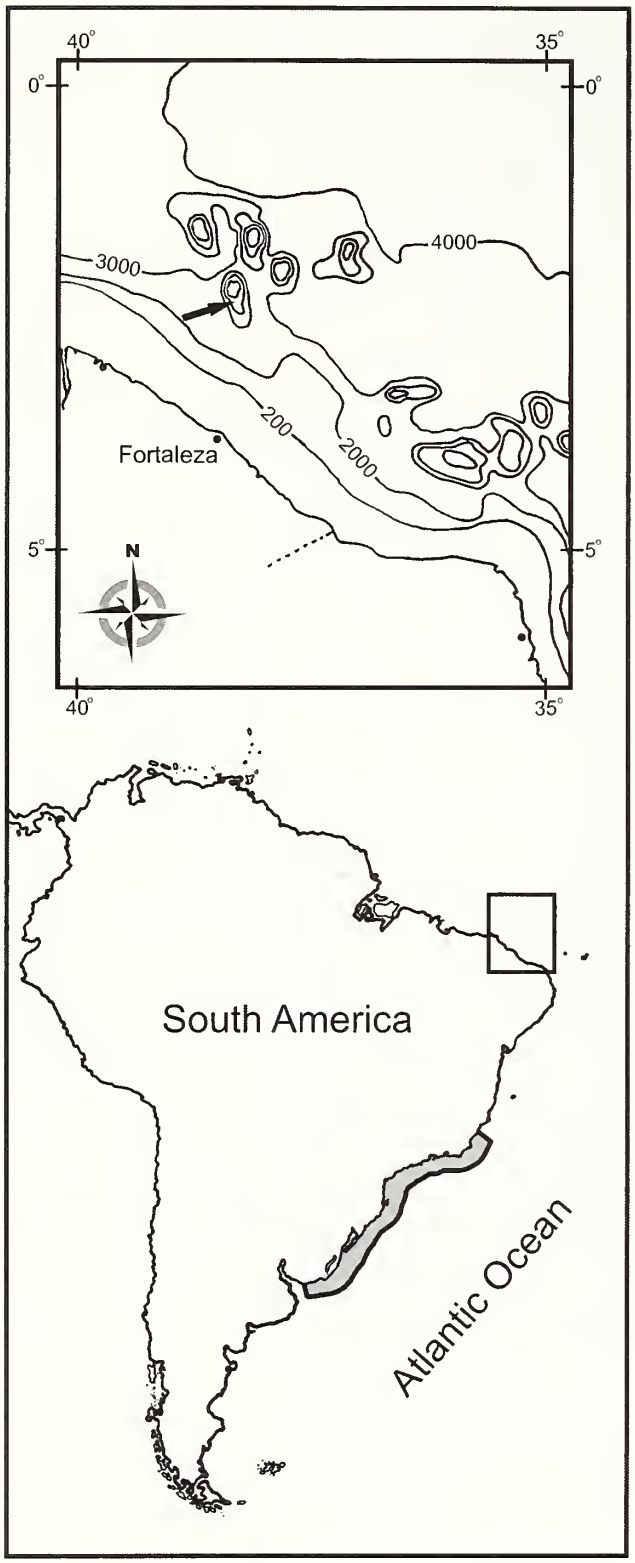


Figure 41. General map showing most of the localities mentioned in text. The gray area indicates the distribution of *N. juani* new species. On top, detail of Canopus Bank area, the black arrow indicates the type locality of *N. laurae* new species.

marginal ribs and smooth margins, as well as the fused umbilical and parietal calluses. *Notocochlis laurae* new species is comparable to *Notocochlis guesti* (Harasewych and Jensen, 1984) (Figures 9–11, 16), which occur from Bermuda to Colombia in moderate deep water (live 201 m). The two species differ, however, in shell shape, color pattern, and operculum sculpture. Individuals in the new species have a higher spire, with the color pattern consisting of an irregular brown band above milk white background without flammules. *Notocochlis guesti* shows one or two spiral bands of brown dots or flammules. The operculum of *N. laurae* new species has two marginal ribs of the same size with an angulated profile, a groove as wide as both marginal ribs together, and the inner margin not serrate. *Notocochlis guesti* has the second marginal rib three times wider than the first, forming a broad plateau and a groove slightly narrower than the second rib. In addition, the inner margin is strongly serrate.

The comparable South Atlantic species belonging to the same genus is *Notocochlis isabelleana* (d'Orbigny, 1840) (Figures 12–14). In addition to the different coloration, *N. laurae* new species is almost twice as large as *N. isabelleana*, which also has a quadrangular profile with a prominent shoulder and higher spire, while the new species is higher than wider, with a shallower suture and thicker basal lip. The opercula in the two species are also quite different, with the operculum in the new species having two well defined marginal ribs, while the operculum of *N. isabelleana* has only one. Finally, there is a significant geographical disjunction between both species, since *N. laurae* new species is a deep water species (~250 m) from off northeastern Brazil, while *N. isabelleana* is a common shallow water species (0–100 m) from the Argentine malacological province.

Genus *Natica* Scopoli, 1777

Type Species: *Natica vitellus* (Linnaeus, 1758) by subsequent designation (Anton, 1838).

Natica juani new species
(Figures 21–28, 30, 37–40)

Type Species: *Natica menkeana* auct.: Costa, Fortes and Freitas, 1997: 14; Costa, Rios and Calvo, 1997: 16 (non Philippi, 1851).

Diagnosis: Shell small, smooth. Umbilicus wide, open; umbilical callus weak fused with parietal callus; sulcus straight, well developed; funicle obsolete; basal lip thick. Color of white background with axial brownish zig-zag flammules, irregularly spaced and interconnected, covering whole shell. Calcareous operculum with a serrate internal margin, and two thick, sometimes one thinner, cords on external margin.

Description: Shell (Figures 21–24, 27–28, 30) small, thick-walled, up to 14 mm of maximum height, globose, spire short, with about two and half whorls; body whorl well developed; protoconch (Figure 30) of about 1.5 whorls

(950 μm of diameter), smooth, without ornamentation, transition to teleoconch well defined; Suture distinetly impressed. Axial sculpture of oblique incremental growth lines. Parietal eallus thin; lobe of anterior parietal callus weakly defined but large. Umbilicus (Figure 27) wide, always open; umbilical eallus moderate in size, fused with parietal callus, always present; sulcus deep, excavated, straight; fumiele moderately developed; basal lip sharp. Aperture very large, semieireular.

Color (fresh specimens) white baekground with axial brownish zig-zag flammules, irregularly spaeed, intereonnected, forming a network, particularly on middle of last whorl. Some specimens with thin, dark periostracum.

Operculum (Figures 25–26) semicircular, solid, eompletely calcified, paucispiral, closing entire aperture. Internal opereular sculpture of growth lines covering whole surfaee; two well defined marginal ribs, sometimes one extra, thinner, after them, a spiral groove along outer margin; caleified granulose zone on eenter of opereulum; inner margin serrate, outer margin smooth.

Radulae taenioglossate (2-1-R-1-2), rachidian teeth trapezoidal with three eusps, eentral one larger, almost obsolete, lateral cusps smaller, anterior edge of base straight, posterior edge slightly convex eentrally and concave at tips, ending in two weak lateral processes. One lateral tooth on eaeh side; central eusp of lateral teeth twice as large as lateral cusps, inner edge of lateral teeth with conspieuous basal prolongation toward center. Two marginal teeth long, curved toward rachidian tooth; inner marginal tooth bifid with cusps of different sizes, inner eusp smaller (Figures 37–38).

Jaws pyriform; rods elongated, comma-shaped, diagonally arranged (Figures 39–40).

Type Locality: Southern littoral of São Paulo State, Brazil, in ~17–35 m.

Distribution: Rio de Janeiro, Brazil to Urugnay (Figure 41).

Type Material: Holotype, MNRJ 17876, southern littoral of São Paulo State, Brazil, in ~17–35 m, from the digestive tract of *Astropeeten* sp., shrimp net; Paratypes: MNRJ 15029, off Búzios, Rio de Janeiro State, Brazil, 22°42′39.4″ S , 40°40′50.2″ W, 3 shells collected on 03/2007; MNRJ 15030, off Búzios, Rio de Janeiro State, Brazil, 22°41′49″ S, 40°40′29.8″ W, 3 shells eolleeted on 03/2007; MNRJ 15028, off Ilha de Cabo Frio, Arraial do Cabo, Rio de Janeiro State, Brazil, 23°18′00″ S, 40°00′00″ W, fishing vessel Muriaé III coll., 2 speeimens colleeted on 04/1993; MNRJ 17875, between Rasa Is. and Ilha Grande, Rio de Janeiro State, Brazil, fishing vessel Marques Torres coll., 2 shells; collected on 02/1994, from the digestive tract of bat fish *Ogeoeephalus vespertilio* (Linnaeus, 1758); MNRJ 17877, from the type locality, 1 shell; MACN-In 39255, from the type locality, 10 speeimens; MZSP 32274, off Ilha Grande, Rio de Janeiro State, 1 speeimen, dredged on 07/11/1969; MZSP 31946, east of Ilha de Vitória, São Paulo State, 36–40 m, 24 specimens, eolleeted with shrimp net, on 06/1999; MZSP 32103, southeast of Lage de Santos, São Paulo State, 55–62 m, 2 shells, collected with shrimp net, on 10/1999; MZSP 32201, off Itajaí, Santa Catarina State, 26°37′ W, 48°15′ S, 85 specimens, collected by otter trawl, Carlo Magenta leg., 04/1997; MNHNM 15517 MARE, 35°38.2′ S, 53°43′ W to 35°39.4′ S, 53°44.7′ W, 61.5–63 m, 1 speeimen collected on 14/11/05; MNHNM 15520, MARE, 35°24.6′ S, 53°24′ W to 35°26′ S, 53°25.7′ W, 60–61 m, 1 shell collected on 1/10/07; MNHNM 15521, MARE, 35°58.1′ S, 53°52.3′ W to 35°59.4′ S, 53°53.5′ W, 62–63.5 m, 2 shells collected on 3/10/07.

Etymology: Dedicated to Juan Pastorino, son of the junior author.

Other Material Examined: MNHNM 10989, R/V Academik Knipovich, St. 1067, 22–29/4/1967, Okean Dredge, 34°26′ S, 51°48.7′ W, 166 m, (3 shells) collected by V. Scarabino; MNHNM 15514, 12/11/05, MARE, 34°41.7′ S, 52°35.6′ W to 34°43.1′ S, 52°37.0′ W, 66–68 m, (2 shells); MNHNM 15513, collected on 12/11/05, MARE, 34°46.5′ S-52°23.7′ W to 34°44.7′ S, 52°23.5′ W, 101–104.5 m, (1 shell); MNHNM 15515, 12/11/05, MARE, 34°55.8′ S, 52°39.5′ W to 34°57.5′ S, 52°40.0′ W, 80.5–82.5 m, (1 shell); MNHNM 15519, MARE, 34°58.2′ S, 52°30.9′ W to 34°59.4′ S, 52°32.0′ W, 108–106 m, 1 shell collected on 12/11/05; MNHNM 11233 R/V Academik Knipovich, St. 1061, 22–29/4/1967, Okean Dredge, 35°04.0′ S, 52°13.6′ W, 175 m, (2 shells), collected by V. Scarabino; MNHNM 15516 13/11/05, MARE, 35°22.9′ S, 53°18.0′ W to 35°24.5′ S, 53°19.3′ W, 62–63.5 m, (1 shell); MNHNM 15518, 14/11/05, MARE, 35°38.2′ S, 53°43′ W to 35°39.4′ S, 53°44.7′ W, 61.5–63 m, (1 shell); all material, except noted, collected by F. Scarabino on board B/I Aldebarán.

Remarks: The complex coloration pattern, fused umbilieal and parietal calluses, operculum calcareous with serrated internal margin, and up to three marginal ribs, are the features of the new species that allow the inclusion in the genus *Natiea*. The new species is eomparable to *Natica menkeana* Philippi, 1851, which is common in Puerto Rico and rare elsewhere in the West Indies. Aeeording to eomparative material examined, the specimen illustrated by Warmke and Abbott (1962: 96, pl. 17 fig. c), and the original illustration (Philippi, 1851b: pl. 15, fig. 8, reprodueed here in Figure 29), the coloration pattern is the main difference. While *N. menkeana* presents a network of reddish brown markings below the suture and a spiral band below the middle of the body whorl, the new speeies has a subsutural white field, and, after it, a brownish network of zig-zag lines. In addition, the spire is shorter and the fumicle appears to be larger. *Natiea eastrensis* Dall, 1889 appears to be a synonym of *N. menkeana* (A. Kabat pers. eomm., 2011). A syntype is illustrated here in Figures 34–36. The subsutural coloration and a remnant of spiral band below the middle of the body whorl are similar to the original illustration of *N. menkeana* and the specimen illustrated by Warmke and Abbott (1962).

In that same publication, Dall (1889: 294) described *Natica perlineata* as a possible variety of *N. castrensis*. The type material is illustrated here in Figures 31–33. The coloration pattern clearly indicates that *N. perlineata* is not conspecific with *N. menkeana* or *N. jnani* new species.

ACKNOWLEDGMENTS

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LITERATURE CITED

Anton, H.E. 1838. Verzeichnis der Conchylien. Halle, xvi + 110 pp.

Costa, P.M.S., E.C. Rios, and I.S. Calvo. 1997. Moluscos Encontrados no Trato Digestivo do Peixe-Morcego, *Ogcocephalus vespertilio* (Linnaeus, 1758) Coletados na Costa do Rio de Janeiro. Siratus, São Paulo 3(13): 16–19.

Costa, P.M.S., R.R. Fortes, and C.A. Freitas. 1997. Lista de Macromoluscos Coletados por Barcos de Pesca de Arrastão ao Largo da Costa do Estado do Rio de Janeiro, Sudeste do Brasil. Siratus, São Paulo 3(13): 14–15.

Dall, H. 1889. Reports on the results of dredgings, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U. S. Coast Survey Steamer 'Blake'. Bulletin of the Museum of Comparative Zoology 18: 1–492, pls. 10–40.

Pastorino, G. 2005. Recent Naticidae (Mollusca: Gastropoda) from the Patagonian coast. The Veliger 47: 225–258.

Philippi, R.A. 1851a. Centuria quarta testaccorum novorum. Zeitschrift für Malakozoologie 8: 39–48.

Philippi, R.A. 1851b. Die Gattung *Natica* und *Amaura*. In: Systematisches Conchylien-Cabinet von Martini und Chemnitz, vol. 2, pls. A, 13–18.

Rios, E.C. 1994. Seashells of Brazil. 2nd. ed.. Fundação da Universidade do Rio Grande, Rio Grande. 368 pp.,113 pls.

Eosipho zephyrus, a new species (Gastropoda: Buccinidae) from deep water off Chile

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ABSTRACT

Eosipho zephyrus, a new deep-water species from off the Chilean coast is described. Protoconch morphology distinguishes the new species from *Cantharus aldermenensis* Powell, 1971, a species commonly placed in the genus *Eosipho* Thiele, 1929. It is the first record of a member of the "*Eosipho aldermenensis* group" in the eastern Pacific. Generic allocation in *Eosipho* Thiele, 1929 versus in *Manaria* Smith, 1906 is briefly discussed. The presence of a third cusp on the lateral teeth of the radula is observed, compared to the same phenomenon in *Manaria* Smith, 1906 and *Colus* Röding, 1786, and considered to be an atypical morphology within the group rather than a feature warranting additional taxonomic separation.

Additional keywords: Manaria, radula, variability, biodiversity, Eastern Pacific

INTRODUCTION

The coastal zone of north to south-central Chile, strongly influenced by wind-driven upwelling, is one of the areas with the highest known primary production rates in the world (Daneri et al., 2000). Consequently, this area of the southeastern Pacific Ocean harbors a vast pelagic and benthic biomass. However, in spite of proof that the benthic fauna is rich in endemic species, many species are still unstudied, undescribed, or unknown. For a brief history and overview of past and recent expeditions and malacological investigations offshore the Chilean coast we refer to Fraussen and Sellanes (2008: 97).

Fraussen and Sellanes (2008) treated some deep-water species of the genus *Aeneator* Finlay, 1927 and a species from the Concepción Methane Seep area (or CMSA) belonging to the genus *Kryptos* Jeffreys in Dautzenberg and Fischer, 1896. The goal of this second paper is to continue adding to the knowledge of the Buccinidae from off Chile with the description of a new species and interpreting it in a wider context by comparing with Indo-West Pacific relatives. It belongs to what we call the "*Eosipho aldermenensis* group". Species belonging to, or assigned to, *Eosipho* are known from the western Atlantic and from the Indo-West Pacific; the *Eosipho aldermenensis* group, however, was until now known only from the Indo-West Pacific. The present new species is the first member of the genus known to occur in the eastern Pacific.

Tropical deep-water Buccinidae are taxonomicaly a rather puzzling group, not the least the species belonging to *Eosipho* Thiele, 1929 and *Manaria* Smith, 1906. Both genera are very similar and it is still a question whether *Cantharus aldermenensis* Powell, 1971 and related species, including the new species described herein, belongs to *Eosipho* or to *Manaria*. We follow the opinion of Bouchet and Warén (1986: 466, 469), retaining this species tentatively in the genus *Eosipho*. Strong evidence exists that the *Eosipho aldermenensis* group may consist of more than one species (Fraussen and Stahlschmidt, unpublished), and the description of the present new species is a first step towards answering this question.

ABBREVIATIONS

JS: collection of Javier Sellanes, Chile; KBIN: Koninklijk Belgisch Instituut voor, Natuurwetenschappen, Brussels, Belgium; KF: collection of Koen Fraussen, Belgium; MNHN: Muséum national d'Histoire naturelle, Paris, France; MNHNCL: Museo Nacional de Historia Natural, Santiago, Chile; PS: collection of Peter Stahlschmidt, Rohrbach, Germany; lv: live collected specimen; dd: empty shell.

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Subfamily Buccinoidea Rafinesque, 1815

Family **Buccinidae Rafinesque, 1815**

Genus ***Eosipho* Thiele, 1929**

Type Species: *Chrysodomus (Sipho) smithi* Schepman, 1911 (by original designation) (type locality: Indonesia, north of Pulau Talisei, Celebes Sea, 01°58′ N, 125°00′ E, 1165–1264 m, Siboga stn 122).

Remarks: Members of the genus *Eosipho* mainly live in the Indo-West Pacific, with species known from the Mozambique Channel in the west, along Indonesia to the Philippines in the east, from Japan in the north to New Zealand in the south. *Eosipho smithi* (Schepman, 1911) and *Eosipho aldermenensis* (Powell, 1971) are both widespread species. The latter was tentatively placed in this genus by Bouchet and Warén (1986: 469) because of conchological affinities. In the present paper we follow this opinion. Further study (Fraussen and Stahlschmidt, unpublished) may involve the placement of *Eosipho aldermenensis* in the genus *Manaria* Smith, 1906 (type species: *Manaria thurstoni* Smith, 1906, by original designation, from "Gulf of Manar", India). More species with conchological characteristics similar to *Eosipho* were included by Shikama (1977: 16, *pygmaeus*), Bouchet and Warén (1986: 467–469, *coriolis*, *engonia*, *thorybopus*), Okutani and Iwahori (1992: 149–250, *tosaensis*), Fraussen (2001: 1–5, *poppei*) and Fraussen and Hadorn (2005: 107–109, *atlanticus*) as well as members from hydrothermal vents (Okutani and Ohta, 1993: 217–218, *desbruyeresi*; Warén and Bouchet, 2001: 191, *auzendai*).

***Eosipho zephyrus* new species**
(Figures 1–10, 13–14, 17–21)

Description: Shell small for genus (up to 11.7 mm), thin, rather fragile, snow white. Shape broad with short spire, whorls convex, suture distinct. Teleoconch consisting of 4 convex whorls with distinct suture. Protoconch consisting of 1 1/2 glossy, rather convex whorls, tip small, whorls rapidly increasing, last whorl rather inflated, resulting in a flattened protoconch. First teleoconch whorl with 6 broad spiral cords, interspaces of fine but deep lines. Second whorl with 8, penultimate whorl with 10 or 11, broad, flat spiral cords; subsutural spiral cords slightly narrower than abapical ones. Body whorl with 22 spiral cords, 3 or 4 cords on siphonal canal; adapical interspaces fine, abapical interspaces gradually becoming broader; interspaces on base half as broad as spiral cords. Last half of body whorl occasionally smooth above periphery (paratype 2, Figures 3, 4) or entirely smooth (paratype 4, Figures 9, 10), but possibly with some traces of interspaces visible near suture.

First teleoconch whorl with 22, second whorl with 27, fine, slightly curved axial ribs, subsuturally rather weak, abapically gradually becoming stronger; interspaces shallow, rather broad. Penultimate whorl with 18 (paratype 5) to 28 (paratype 2), body whorl with 25–27 such axial cords, gradually becoming weaker, last part of body whorl almost smooth. Aperture oval, columella smooth, glossy, slightly curved; outer lip thin, simple, edge sharp. Siphonal canal short, broad, open.

Operculum (Figure 8) small, thin, transparent, yellowish brown, elongate; nucleus terminal, tip sharp.

Radula (Figures 19–21) typically buccinid. Central tooth tricuspid with rather rectangular base. Lateral teeth variable, atypical of genus, principally bicuspid but with a small additional intermediate cusp.

Type Material: Holotype (MNHNCL 6677) (10.5 mm), southern Chile, off Chiloé, about 42°S, in 500 m, dd; Paratype 1 (MNHNCL 6678) (11.7 mm), same locality as holotype, dd; paratype 2 (KF 5442) (10.5 mm), same locality as holotype, dd. Paratypes 3–4 (MNHNCL 6679–6680) (9.8–10.7 mm), Chile, off Concepción, 'Antarctic Intermediate Water' Cruise, R/V *Vidal Gormáz*, 36°24.12′ S, 73°36.44″ W, in 606 m, lv; paratype 5 (KF 5443) (9.7 mm), same locality as paratypes 3 and 4; paratype 6 (MNHN 24775) (11.8 mm), southern Chile, off Taitao peninsula, INSPIRE Cruise, R/V *Melville*, 46°54.15′ S, 75°35.99′ W, in 497 m, lv; paratype 7 (PS 150133) (11.0 mm), same locality as paratype 6, lv; paratypes 8–10 (KF 6579–6581) (10.7–12.2 mm), same locality as paratype 6, 2 lv, 1 dd; paratype 11 (KBIN) (11.5 mm), same locality as paratype 6, lv; paratypes 12–28 (JS) (8.8–13.2 mm), same locality as paratype 6, 16 lv, 1 dd.

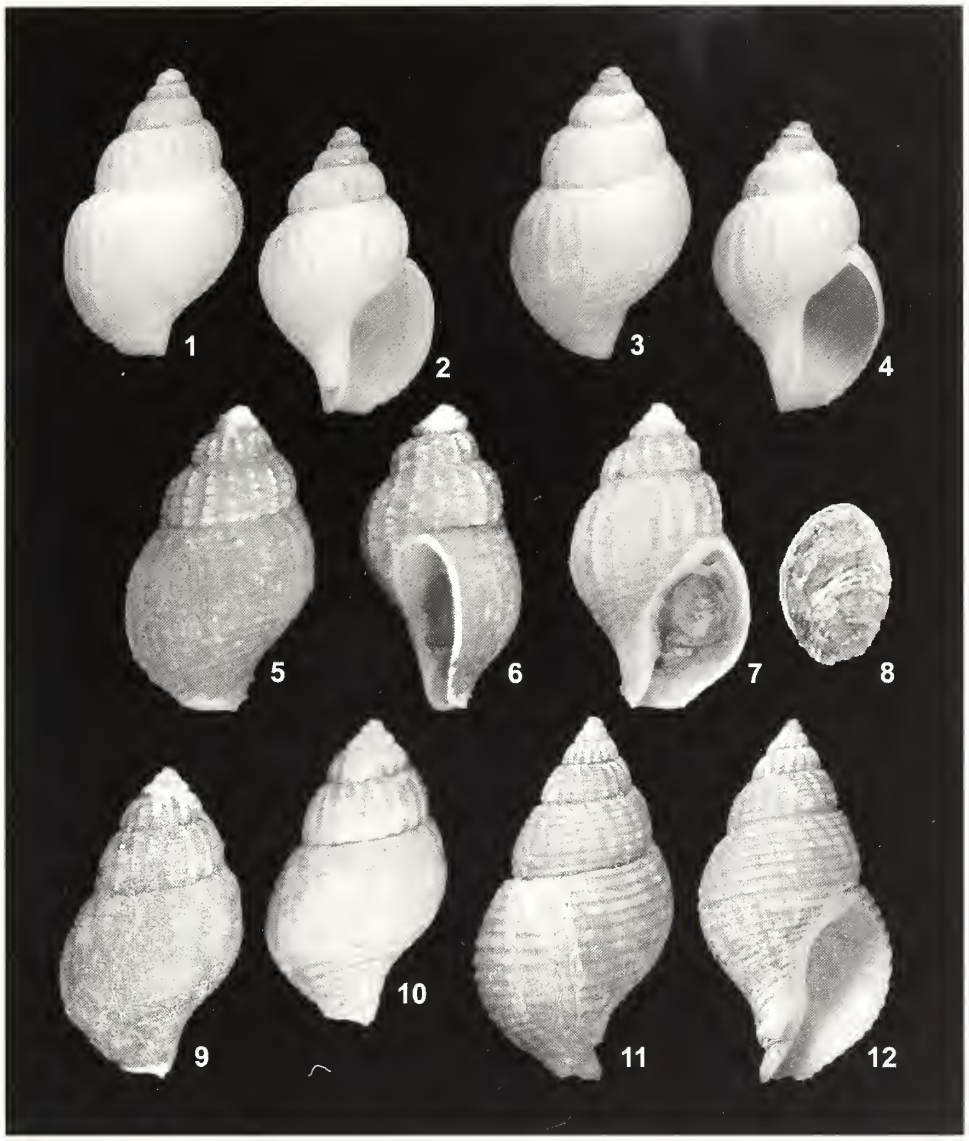
Type Locality: Southern Chile, off Chiloé, around 42° S, upper continental slope, in 500 m.

Range and Habitat: Only known from the type material. Detailed habitat data are not available, but two of the sites (off Concepción and Taitao peninsula), in which the specimens were collected, have been identified as methane seep areas. Live collected shells are covered with a thick, unidentified sponge-like mass (Figures 9, 17–18).

Etymology: *Eosipho zephyrus* new species is named after the Greek god for the west wind Zephyrus, a name used as a noun in apposition. The name is an allusion to the easternmost occurrence of this species, far from the ranges of the other congeneric species in the Indo-West Pacific, as if it were blown to the east by the wind.

Comparative Remarks: *Eosipho zephyrus* new species is characterized by the broad shape with moderately short spire, the convex teleoconch whorls, the weak spiral sculpture consisting of flat cords and narrow interspaces, the broad and blunt protoconch with rapidly increasing whorl size, greenish and rather smooth periostracum and small adult size.

Eosipho zephyrus new species is variable in presence of spiral sculpture (present or absent on the adapical part of the body whorl) and in number of axial ribs (18 to 28 ribs on penultimate whorl).

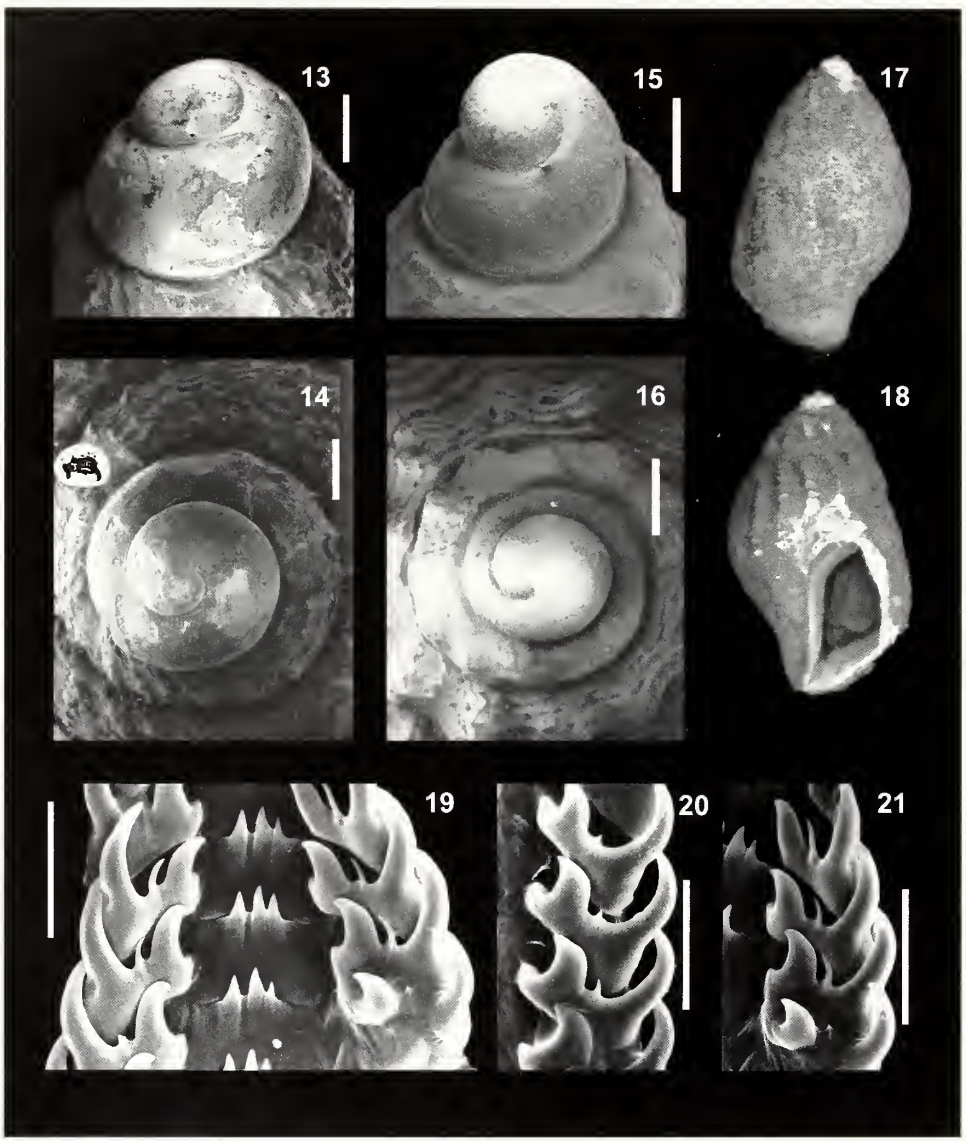


Figures 1–12. *Eosipho* species. **1–10.** *Eosipho zephyrus* new species. **1–2.** Holotype, 10.5 mm, Chile, Chilean upper continental slope, in 500 m, MNHNCL 6677. **3–4.** Paratype 2, 10.5 mm, same locality, KF 5442. **5–7.** Paratype 5, 9.7 mm, Chile, off Concepción, AIW Cruise, 36°24.12′ S, 73°36.44′ W, in 606 m, KF 5443. **8.** Operculum of paratype 5, 2.2 mm, KF 5443. **9.** Paratype 4, 10.7 mm, same locality, MNHNCL 6680. **10.** Same shell, cleaned. **11–12.** *Eosipho aldermenensis* (Powell, 1971), 16.8 mm, East China Sea, off China, in 280–380 m, KF 5244.

The protoconch (Figure 13, 14) is quite atypical of both *Eosipho* Schepman, 1911 and *Manaria* Smith, 1906. While species belonging to these genera have a protoconch consisting of gradually larger, convex whorls (Figure 15, 16), the new species differs in having a bigger last whorl and a flattened appearance.

The radula of *Eosipho zephyrus* new species is atypical of Cominellinae (containing both *Eosipho* Schepman, 1911 and *Manaria* Smith, 1906) by the presence of a third cusp on the lateral teeth (Figures 19–21). This additional cusp is usually small to minute and appears to be an additional rather than a constant presence. Variability in number of rachidian cusps within a single genus is not unusual in Buccinidae: *Neptunea* Röding, 1798 with 3–7 lateral cusps (Golikov 1964: 17, 29–33; Fraussen and Terryn, 2007: 21, 39, 64), *Buccinum* Linnaeus, 1758 with 2–6 lateral cusps (Golikov 1980: 54, 99–104), *Prosipho* Thiele, 1912 with 2–6 lateral cusps (Powell, 1951: 193; Oliver and Picken, 1984: 96; Dell, 1990: 187). The presence of an additional median cusp in Cominellinae is known in *Manaria lirata* Kuroda and Habe in Habe, 1961 (Fraussen and Stahlschmidt, unpublished) and in Buccinulinae in *Drepanodontus* Harasewych and Kantor, 2004 (Harasewych and Kantor, 2004: 7, 12, figs. 36–40).

Eosipho aldermenensis (Powell, 1971) (type locality: "E. of the Aldermen Islands, New Zealand, 366–475 m")



Figures 13–21. *Eosipho* species. **13–14.** *Eosipho zephyrus* new species, protoconch of holotype, scale bar = 300 micrometer, MNHNCL 5866. **15–16.** *Eosipho aldermenensis* (Powell, 1971). Vanuatu (BOA O expedition, station CP2319), MNHN. Scale bar = 300 µm. **17–21.** *Eosipho zephyrus* new species. **17–18.** Paratype 3, 9.8 mm, Chile, off Concepción, RIW Cruise, 36°24.12′ S, 73°36′44 W, in 606 m, MNHNCL 6679. **19–21.** Radula of holotype. Scale bar = 40 µm.

(Figures 11–12, 15–16), a widespread species in the Indo-West pacific, differs in having a smaller protoconch compared to shell length, broader spiral cords with broader interspaces, a lower number of axial ribs and a larger adult size. Some evidence may exist (Fraussen and Stahlschmidt, unpublished) that several Indo-West Pacific records assigned to *Eosipho aldermenensis* belong to distinct species. A thorough study of this complex is beyond the scope of the present paper, and we hereby tentatively regard "*aldermenensis*" as a group and we use this name for the Indo-West Pacific species.

Manaria brevicaudata (Schepman, 1911) (type locality: Borneo, north off Kagayan de Sulu Island, Flores Sea, SIBOGA stn. 45, 07°24′ S, 118°15′ E, 794 m) is similar in spiral sculpture (fine spiral grooves), in variability (absence or presence of spiral sculpture on the adapical part of the body whorl) and periostracum (greenish and smooth) but differs in having a slender shape with a high spire, a slightly longer siphonal canal, a lower number of axial ribs and a larger adult size. The protoconch of *Manaria brevicaudata* is unknown, all specimens studied by us have eroded protoconch.

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LITERATURE CITED

Bouchet, P. and A. Warén. 1986. Mollusca Gastropoda: Taxonomical notes on tropical deep water Buccinidae with descriptions of new taxa. Résultats des Campagnes MUSORSTOM. I & II. Philippines, tome 2. Mémoires du Museum national d'Histoire naturelle, 1985, série A, Zoologie 133: 457–499.

Daneri, G., V. Dellarossa, R. Quiñones, B. Jacob, P. Montero, and O. Ulloa. 2000. Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. Marine Ecology-Progress Series 197: 41–49.

Dell, R.K. 1990. Antarctic Mollusca, with special reference to the fauna of the Ross Sea. The Royal Society of New Zealand, Bulletin 27: 1–311.

Fraussen, K. 2001. A new *Eosipho* (Gastropoda: Buccinidae) from the Philippine Islands. Gloria Maris 39 (5–6): 90–97.

Fraussen, K. and R. Hadorn. 2005. A new species of *Eosipho* (Gastropoda: Buccinidae) from Guadeloupe, Western Atlantic. Novapex 6: 107–109.

Fraussen, K. and J. Sellanes. 2008. Three New Buccinid Species (Gastropoda: Neogastropoda) from Chilean Deep-Water, Including One from a Menthane Seep. The Veliger 50: 97–106.

Fraussen, K. and Y. Terryn. 2007. The Family Buccinidae: Genus Neptunea. In: G. T. Poppe and K. Groh (eds.) A Conchological Iconography. ConchBooks, Hackenheim, 166 pp., 154 pl.

Golikov, A.N. 1963. Gastropod mollusks of the Genus *Neptunea* Bolten. Fauna of the USSR, Mollusks. USSR Academy of Science 5(1): 1–183.

Golikov, A.N. 1980. Buccininae mollusks of the World Ocean. Fauna of the USSR, Mollusks. USSR Academy of Seience 5(2): 1–465.

Habe, T. 1961. Coloured illustrations of the shells of Japan. 2. Hoikusha, Osaka, 183 pp.

Harasewych, M.G. and Y.I. Kantor. 2004. The deep-sea Buccinoidea (Gastropoda: Neogastropoda) of the Scotia Sea and adjacent abyssal plains and trenches. The Nautilus 118: 1–42.

Okutani, T. and A. Iwahori. 1992. Noteworthy gastropods collected from bathyal zone in Tosa Bay by the R/V Kotaka-Maru in 1987 and 1988. Venus 51: 235–268.

Okutani, T. and S. Ohta. 1993. New buccinid and turrid gastropods from North Fiji and Lau basins. Venus 52: 217–221.

Oliver, P.G. and G. Picken. 1984. Prosobranch gastropods from Signy Island, Antarctica: Buccinacea and Muricacea. British Antarctic Survey, Bulletin 62: 95–115.

Powell, A.W.B. 1951. Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. Discovery Reports 26: 47–196.

Powell, A.W.B. 1971. New Zealand molluscan systematics with descriptions of new species: part 7. Records of the Auckland Institute and Museum 8: 209–228.

Powell, A.W.B. 1979. New Zealand Mollusca. Marine, Land and Freshwater Shells. Auckland Institute and Museum, Collins, Australia, 474 pp.

Röding, P.F. 1798. Museum Boltenianum sive catalogus cimeliorum e tribus regnis naturæ quæ olim collegerat Joa. Fried Bolten, M. D. p. d. per XL. annos proto physicus Hamburgensis. Pars secunda continens conchylia sive testacea univalvia, bivalvia & multivalvia. 1–199 pp.

Schepman, M.M. 1911. Prosobranchia of the Siboga Expedition. Part 4: Rachiglossa. Siboga Expeditie: 247–364.

Shikama, T. 1977. Description of new and noteworthy Gastropoda from Western Pacific and Indian Oceans. Science Reports of Yokohama National University (sect. 2) 24: 9–24.

Smith, E.A. 1906. Natural history notes from R.I.M.S. 'Investigator'. Series 3 (10). On Mollusca from the Bay of Bengal and the Arabian Sea. The Annals and Magazine of Natural History (serie 7) 18(105): 157–175.

Thiele, J. 1912. Die antarktischen Schnecken und Muscheln. Deutsche Südpolar-Expedition 1901–1903 (13): 183–285.

Thiele, J. 1929. Handbuch der Systematischen Weichtierkunde. Gustav Fischer, Jena, 376 pp.

Warén, A. and P. Bouchet. 2001. Gastropoda and Monoplacophora from hydrothermal vents and seeps; new taxa and records. The Veliger 44: 116–231.

Land slugs (Gastropoda: Pulmonata) on birds demonstrate dispersal potential

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ABSTRACT

We deseribe the discovery of two slugs, *Arion subfuscus* and *Deroceras reticulatum*, on living adult birds eaptured for banding at Powdermill Nature Reserve, Rector, Pennsylvania. The presence of slugs on birds suggests that bird transport might play a role in slug dispersal.

Additional keywords: Gray fieldslug, *Deroceras reticulatum*, dusky arion slug, *Arion subfuscus*, eommon yellowthroat, *Geothlypis trichas*, northern saw-whet owl, *Aegolius acadicus*.

INTRODUCTION

Although land snails and slugs are quintessentially slow-moving creatures, their ability to colonize new areas indicates that they do, in fact, disperse. Some terrestrial gastropod species have evidently dispersed considerable distances, including across inhospitable bodies of salt water (Rees, 1965; Vagvolgyi, 1975; Wesselingh et al., 1999). Other than direct locomotion or transport by humans (including as eggs), possible agents of dispersal include water (Smith and Djajasasmita, 1988), wind (Kirchner et al., 1997), and other organisms such as birds (Dundee et al., 1967; Purchon, 1977: 383; Wesselingh et al., 1999; Wada et al., 2011).

Direct evidence for these dispersal mechanisms remains limited, and we are not aware of any published evidence for slug dispersal via wind or water. Most evidence for gastropod dispersal via other organisms pertains to shelled snails. We are aware of only two previous reports of slugs being carried by non-human animals: one report of a slug in the fur of a house cat (McMillan, 1989) and one report of slugs being caught and subsequently dropped by bats (Johnston, 1992). This paper presents the first known report of slugs on living adult birds.

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MATERIALS AND METHODS

In 2003 and 2004, two land slugs were found on birds trapped in mist nets at Powdermill Nature Reserve (Rector, PA; 40.1636° N, 79.2668° W). The birds were trapped by R.M. as part of the Powdermill Nature Reserve (PNR) bird banding program. The nets were located in a wet shrub-scrub habitat dominated by willows. Cursory examination of all birds for ectoparasites is a routine part of the banding procedure, as is documentation of molt, and, during examination, the slugs were discovered on two species of birds. The two birds upon which the slugs were found were a common yellowthroat (*Geothlypis trichas* (Linnaeus, 1766)) and a northern saw-whet owl (*Aegolius acadicus* (Gmelin, 1789)). The common yellowthroat was captured on September 14, 2003, and the northern saw-whet owl was captured on November 11, 2004 at night. The slugs were sent for identification and deposited in the collection at the Section of Mollusks, Carnegie Museum of Natural History (CM).

RESULTS

The two birds upon which the slugs were found were a common yellowthroat and a northern saw-whet owl. The slug on the common yellowthroat was *Deroceras reticulatum* (Müller, 1774) (CM 66603) and was found among the bird's body feathers. This slug was a juvenile, 7.4 mm long (in alcohol), and was identified as *D. reticulatum* by its paler tan color, reticulated markings, and presence of a pale pneumostome border (mucus color was not noted before preservation). The slug on the northern saw-whet owl was *Arion subfuscus* (Draparnaud, 1805) (CM103313), and it also was found among the bird's body feathers. This slug was also a juvenile, 10.4 mm long (in alcohol), and was identified as *A. subfuscus* by the pale sole and presence of 15 rows of tubercles between the lateral bands (mucus color was not noted before preservation). The common yellowthroat was high in the net when it was captured; the owl

was in the lower shelf of the net and in contaet with the ground.

DISCUSSION

The presenee of the slugs within the plumage of the birds suggests that these migrants might have been aetively transporting the slugs when they were caught. We aeknowledge the possibility that the slugs crawled onto the birds after they were trapped in the mist net; however, two factors suggest that this is unlikely. First, during R.M.'s 25+ years of mist-net banding at PNR, he has never observed a slug or snail on a mist net. Seeond, one of the birds, the eommon yellowthroat, was caught high in the net, about 1.5 m off the ground.

While both slug species were already known in the vieinity of PNR, the possibility of transport by migratory birds has implieations for distribution and gene flow of slugs, as it has for other gastropods (Miura et al. 2011). The faet that this is the first report of slugs being found on living adult birds suggests that if dispersal by birds does oeeur, it is rare (or rarely documented). Kew (1893: 175), in a chapter on dispersal of slugs, speculated that slug dispersal by birds, if it occurred, would be rare, but did not eite any actual examples of sueh dispersal. However, given the wide ecological and migratory ranges of many bird speeies, even very oeeasional transport by birds eould allow some slugs to spread over mueh greater distanees than would otherwise be possible.

The ranges and habitats overlap for the slugs and the birds. In addition, both slug species ascend trees or vegetation during moist weather (Jennings and Barkham, 1975; pers. obs.), which might inerease chances of an encounter with a bird. *Deroceras reticulatum*, originally native to Europe, is now introduced in most temperate and subtropical regions throughout the world (Roth and Sadeghian, 2003; Forsyth, 2004). It occurs in open and modified environments ineluding agricultural land, roadsides, hedges, and grasslands, avoiding woodlands (Kerney and Cameron, 1979; Wiktor, 2000; Barker, 2002: 422; Forsyth, 2004). The common yellowthroat extends throughout North and Central Ameriea and it inhabits thick, tangled vegetation (particularly in wet areas) (Guzy and Ritchison, 1999; GBIF, 2011).

The ranges of *Arion subfuscus* and the northern saw-whet owl also overlap (Rasmussen et al., 2008; NatureServe, 2011), as do their habitats. *Arion subfuscus*, native to Europe where it mainly inhabits deeiduous and coniferous forests and sometimes pastures (Wiktor, 1983), is introduced in northeast and northwest North America. Although it is not commonly associated with humans in most of Europe, in western Britain and in North America, in addition to oecurring in deeiduous and coniferous forests, it is frequently found in gardens and on roadsides near human settlements (Chichester and Getz, 1973; Kerney and Cameron, 1979; Kerney, 1999; Forsyth, 2004). Saw-whet owls are found in a variety of woodlands and forested habitats, with densities highest in coniferous forests, especially along riparian corridors (Johnson and Anderson, 2003; Rasmussen et al., 2008).

Because the geographical ranges and habitats of the slugs and birds overlap, the current distribution of these slugs in North America might be partially the result of bird dispersal. Dispersal of the slugs by birds might be especially relevant to their distribution given that they are not native to North America and have been present on the continent for relatively short periods of time (160–170 years (Pilsbry, 1948)).

Two other examples of interactions between slugs and birds, while not involving dispersal, indicate that contact oceurs between birds and slugs, demonstrating the plausibility of slugs attaching to feathers of living birds. Livezey et al. (2008) reported a barred owl capturing and eating slugs. Biasiolli (2009) suggested that an arionid slug, possibly *Arion subfuscus*, was eating a living nestling black-throated blue warbler while the female bird continued to attend to the nest. During these interactions, other slugs, had they been present, might have become entangled in the feathers of the birds.

The two slugs reported here were alive when they were discovered. However, it is unclear how long the slugs had been on the birds prior to their discovery. The inereased humidity inside a bird's feathers, coupled with the ability of many slugs to survive significant desiccation (e.g., up to 50% of their body weight (Runham and Hunter, 1970: 72)), might allow slugs to survive on birds far longer than otherwise expected. On the other hand, birds might be expected to remove slugs through preening.

Relatively little is known about the distribution and transport of gastropods (espeeially slugs) by other animals. It is likely that transport by birds is infrequent, given the lack of any prior observations of slugs on living adult birds. For example, R.M. has banded hundreds of thousands of birds (ineluding >2,500 common yellowthroats and >100 northern saw-whet owls). Each bird is examined for eetoparasites, as well as signs of active molt, but these are the first times slugs have been noticed. The presence of small slugs deep within the plumage of other birds handled at Powdermill, however, cannot be ruled out, beeause the examinations may not be detailed enough (especially on busy banding days) to deteet slugs deep in the feathers or otherwise obseured (indeed, the soft, feather-covered blobs removed from the birds were not initially recognized as slugs until they started to move). It seems reasonable that speeies of bird such as the eommon yellowthroat and northern saw-whet owl, which forage (or attaek prey) in dense, often damp vegetation on and near the ground, might come into direet eontact with slugs that then become attached to the bird's plumage. Especially in the case of birds that are actively migrating, it is conceivable that the urge to migrate when conditions are favorable might supersede maintenanee behavior activities, such as preening. We know that at least some of the northern saw-whet owls eaptured at Powdermill at night were, in faet, actively

migrating when they were netted (Powdermill Nature Reserve, 2007).

Range expansion via bird transport has been reported for snails (Wesselingh et al., 1999). Our observations of slugs on living adult birds suggest that this dispersal mechanism might also be important to the establishment and expansion of at least some slug populations, which, like many snails, are hermaphroditic and many can self-fertilize. Further investigation into the prevalence of slug transport by birds could be useful in predicting the possible spread of invasive slug species.

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LITERATURE CITED

Chichester, L.F. and L.L. Getz. 1973. The terrestrial slugs of northeastern North America. Sterkiana (51): 11–42.

Biasiolli, T.G. 2009. Depredation of black-throated blue warbler nestlings by an introduced slug (Arionidae). Wilson Journal of Ornithology 121: 422–423.

Barker, G.M. 2002. Molluscs as Crop Pests. CABI Publishing, New York. i–xii+1–468 pp.

Dundee, D.S., P.H. Phillips, and J.D. Newsom. 1967. Snails on migratory birds. The Nautilus 80: 89–91.

Forsyth, R.G. 2004. Land Snails of British Columbia. Royal BC Museum, Victoria. 188 pp.

GBIF (Global Biodiversity Information Facility). 2011. *Geothlypis trichas* (Linnaeus, 1766). http://data.gbif.org/. [accessed 13 November 2011].

Guzy, M.J. and G. Ritchison. 1999. Common Yellowthroat (*Geothlypis trichas*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/species/448 [accessed 13 November 2011].

Jennings, T.J. and J.P. Barkham. 1975. Food of slugs in mixed deciduous woodlands. Oikos 26: 211–221.

Johnson, A.S. and S.H. Anderson. 2003. Conservation Assessment for the Northern Saw-whet Owl in the Black Hills National Forest, South Dakota and Wyoming. United States Department of Agriculture, Black Hills National Forest, Custer, South Dakota. 27p. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsm9_012447.pdf [accessed 13 November 2011].

Johnston, D. 1992. Indiscriminate prey-capture in an opportunistic gleaner, the pallid bat *Antrozous pallidus*. Bat Research News 33: 60–61.

Kerney, M.P. and R.A.D. Cameron. 1979. A field guide to the land snails of Britain and North-west Europe. Collins, London, 288 pp.

Kerney, M. 1999. Atlas of the Land and Freshwater Molluscs of Britain and Ireland. Harley Books, Colchester. 261 pp.

Kew, H.W. 1893. The dispersal of shells: an inquiry into the means of dispersal possessed by fresh-water and land Mollusca. Kegan Paul, Trench, Trübner and Co., Ltd., London, xiv + 291 pp.

Kirchner, Ch., R. Krätzner, and F.W. Welter-Schultes. 1997. Flying snails – how far can *Truncatellina* (Pulmonata: Vertiginidae) be blown over the sea? Journal of Molluscan Studies 63: 479–487.

Livezey, K.B., M.F. Elderkin, P.A. Cott, J. Hobbs, and J.P. Hudson. 2008. Barred owls eating worms and slugs: the advantage in not being picky eaters. Northwestern Naturalist 89: 185–190.

McMillan, N.F. 1989. Cat carrying a slug. Conchologist's Newsletter (111): 245–246.

Miura, O., M.E. Torchin, E. Bermingham, D.K. Jacobs, and R.F. Hechinger. 2011. Flying shells: historical dispersal of marine snails across Central America. Proceedings of the Royal Society B, published online 14 September 2011, doi: 10.1098/rspb.2011.1599.

NatureServe. 2011. *Arion subfuscus*. http://www.natureserve.org/explorer. [accessed 13 November 2011].

Pilsbry, H.A. 1948. Land Mollusca of North America (North of Mexico). Academy of Natural Sciences of Philadelphia, Monograph 3, volume II, part 2. i–xlvii, 521–1113.

Powdermill Nature Reserve. 2007. Pictorial highlights, late fall 2007. http://www.powdermillare.org/highlights/2007/november.aspx [accessed 13 November 2011].

Purchon, R.D. 1977. The Biology of the Mollusca, 2nd edition. Pergamon Press, Oxford, xxv + 560 pp.

Rasmussen, J.L., S.G. Sealy, and R.J. Cannings. 2008. Northern saw-whet owl (*Aegolius acadicus*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/species/042 [accessed 13 November 2011].

Rees, W.J. 1965. The aerial dispersal of Mollusca. Presidential address. Proceedings of the Malacological Society of London 36: 269–282.

Roth, B. and P.S. Sadeghian. 2003. Checklist of the land snails and slugs of California. Santa Barbara Museum of Natural History Contributions in Science 3: 1–81.

Runham, N.W. and P.J. Hunter. 1970. Terrestrial slugs. Hutchinson University Library, London. 184 pp.

Smith, B.J. and M. Djajasasmita. 1988. The land molluscs of the Krakatau Islands, Indonesia. Philosophical Transactions of the Royal Society of London, Series B 323: 379–400.

Vagvolgyi, J. 1975. Body size, aerial dispersal, and origin of the Pacific land snail fauna. Systematic Zoology 24: 465–488.

Wada, S., K. Kawakami, and S. Chiba. 2011. Snails can survive passage through a bird's digestive system. Journal of Biogeography. doi: 10.1111/j.1365-2699.2011.02559.x, 5 pp.

Wesselingh, F.P., G.C. Cadée, and W. Renema. 1999. Flying high: on the airborne dispersal of aquatic organisms as illustrated by the distribution histories of the gastropod genera *Tryonia* and *Planorbarius*. Geologie en Mijnbouw 78: 165–174.

Wiktor, A. 1983. The slugs of Bulgaria (Arionidae, Milacidae, Limacidae, Agriolimacidae – Gastropoda Stylommatophora). Annales Zoologici 37: 71–206.

Wiktor, A. 2000. Agriolimacidae (Gastropoda: Pulmonata) - a systematic monograph. Annales Zoologici 49: 347–590.

The case of the abducted *The Nautilus* papers

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The purpose of this note is to make known the existence on the Internet, for over a year, of two papers on which authorship had been changed from previously published originals. Although now removed from the Internet, these were downloadable .pdf files and may have been downloaded and/or printed from those .pdf files.

In 2005, Petit was asked for assistance in identifying some deep-water Cancellariidae by Lima, then a Brazilian malacology student. As a result, two papers based on that material were published in *The Nautilus* in 2007. One of them was coauthored by Lima's professor, José Carlos Nascimento de Barros (hereafter Barros) and Petit. On the other paper, Lima was the first author with Barros and Petit.

For the 2010 *Semana Nacional de Ciência e Tecnologia* (2010 National Week of Science and Technology) a program with abstracts, but also including complete papers, was placed onto the Internet. Articles in .pdf format had the heading *X Jornada de Ensino, Pesquisa e Extensão – JEPEX 2010 – UFRPE: Recife, 18 a 22 de outubro* (X Meeting of Teaching, Research and Continuing Education).

The second of the two papers mentioned above, authored by Lima, Barros, and Petit, was copied in .pdf format in those online *Jornada* abstracts, with no mention of *The Nautilus* or original authorship. Seven authors are listed: Guilherme Lima Moraes, José Carlos Nascimento de Barros, Jonata de Arruda Francisco, Silvio Felipe Barbosa de Lima, Severino Adriano de Oliveira Lima, Paulo Henrique Gomes da Paixão, and Nefi Medeiros Fernandes. Institutional affiliation was denoted by superscript numbers corresponding to addresses at the bottom of the page. By the time this appeared, Lima was no longer a student in Recife, but at a different university in Paraiba. It must be mentioned that Lima was unaware that this paper had been changed and posted online until this was called to his attention in July 2011. Barros is listed as second author and the other five persons listed are believed to be his students, as was Lima before he moved.

That *The Nautilus* paper is not copied in its entirety, but what is copied is almost verbatim. Copied are the Introduction, Systematics, and Discussion. The Description is only about half copied. Type Material, Type Locality, Geographical Distribution, Etymology, Remarks, and Material Examined are not included. However, all data concerning the holotype is given in the figure caption. The figure and its caption are copied without change. References cited are deleted in the text, with numbers substituted that correspond to numbered References at the end.

The first paper mentioned above, by Barros and Petit, was copied in a similar manner. Figures 9–11 were not reproduced as they are of a different species. Authors shown on this copy were: Néfi de Medeiro Fernandes, Guilherme Lima Moraes, Jonata de Arruda Francisco, and José Carlos Nascimento de Barros.

When this matter came to our attention in June 2011, Lima was contacted by Petit. He knew nothing of the matter but promised to investigate although he was no longer in Recife.

In early December 2011, it was noted that these papers were still on the Internet. Once again Lima was contacted. Petit asked Lima to advise Barros and the people in charge of keeping these articles on the Internet of possible consequences if they were not removed immediately. As even that had no effect, the situation was explained in rather stronger terms, which Lima passed on and the papers were then taken off the Internet sometime between 21 December and 27 December 2011.

One of the problems with these copied papers is the matter of them having wrong authorship. A more serious problem is that any hard copies printed from these .pdf files would appear to be Code-compliant original papers. All features needed for validation of the names were copied.

Although these two transformed papers are not published under the provisions of the Code, there is nothing in their appearance to indicate that they were not issued in print. Such listings on the Internet can lead to the misattribution of authorship and incorrect dating of nomina when picked up by sources scavenging the Internet for data used in compilation of lists and data bases. There are now companies publishing entire "books" consisting entirely of material uncritically taken from the Internet (Petit, in preparation).

The PDF papers that are the subject of this article are not listed in the Literature Cited as to do so would give them an undeserved legitimacy.

LITERATURE CITED

Barros, J. C. N. de and R. E. Petit. 2007. A new species of *Microcancilla* (Gastropoda: Cancellariidae) from the continental slope off northeastern Brazil. The Nautilus 121: 95–98.

Lima, S. F. B. de, J. C. N. de Barros and R. E. Petit. 2007. A new species of *Gerdiella* (Gastropoda: Cancellariidae) from the South Atlantic Ocean off Brazil with discussion of an undescribed species. The Nautilus 121: 99–103.

Book Review

Gofas, S., D. Moreno, and C. Salas (eds). 2011. Moluscos Marinhos de Andalucia. 2 Volumes. Servicio de Publicaciones e Intercambio Científico, Universidad de Málaga. Xvi, pp 1–342 pp; xii, pp. 343–798. Hardcover. Price €150 from publisher. €228/$296 at www.nhbs.com.

The marine malacofauna of the European-Mediterranean area is possibly one of the best documented on the globe. Comprehensive text-only treatments date back at least to Weinkauff (1867, 1868). An early illustrated work includes Bouquoy et al.'s (1882–1886) *Les Mollusques du Roussillion* covering the famous Banyuls-sur-Mer, France, field station. Subsequent comprehensive works include Nordsieck (1968, 1969, 1972, 1982) with its unmistakable line drawings, Poppe and Goto (1991, 1992), and the fairly recent Cossignani and Ardovini (2011). There is no shortage on specialty volumes either, including Ardovini and Cossignani (1999), the atlas series (e.g. Giannuzzi-Savelli et al., 1994), or the classic Opisthobranchia tome by Schmeckel and Portman (1982) with its stunning illustrations. Not to mention the more limited treatments such as D'Angelo and Garguillo (1978).

On the face of it, what could a regional guide to Andalusia (Spanish coast from the southeastern border to Portugal past Gibraltar including a quarter of the Mediterranean coast of Spain) possibly add to this already impressive library? Far more than the title might suggest.

The overall work is a two volume set, 11 1/3 × 9 ½ inches = 28.3 × 23.7 cm, i.e., slightly taller than US letter-size paper and significantly wider. The larger Volume 1 contains a 50-page introduction to the marine environment and its various biomes, the Andalusian region, as well as an overview on molluscan systematics and diversity. Groups covered are Solenogastres, Caudofoveata, Polyplacophora, and Gastropoda up to Conidae. Volume 2 contains the remaining Gastropoda, as well as Bivalvia, Scaphopoda, and Cephalopoda.

The introduction to each class contains 5–7 pages of text including anatomical drawings and scanning electron micrographs (SEM) of the radula. The treatments of the families by one, two, or three Spanish specialists are moderately detailed. Each family is given a 1–2 page introduction, including a section with key references. The species treatments are in a two-column format with illustrations along the outer margin and the text toward the center. Generic diagnoses are not provided. Species name and authority are given, but synonyms are not indicated. About three species are treated on each page covering the description of the shell, taxonomic remarks, and indications on habitat and distribution. There are several aspects that help render this volume a veritable treasure trove, both for workers in the Mediterranean and for a global audience.

First, the comprehensive treatment of the micromollusks. As it has become more common in recent publications, those are shown in detail. Even most Scissurellidae and Anatomidae are correctly identified, with the exception of *Anatoma crispata* (Fleming, 1828) on page 30, which in fact shows an *Anatoma teuniseulpta* (Seguenza, 1877); see Høisaeter and Geiger (2011) for details.

Another aspect to be emphasized are the multiple illustrations for many taxa, particularly for micromollusks. In some cases, multiple specimens are shown, but in many cases complementary documentation is also presented. For instance, the general shell morphology of eulimids associated with a close-up image showing microsculpture. Or photographs of pyramidellids with complementary SEM of the apex with protoconch.

Last but not least, the many photographs of live animals are worth noting. While they are becoming more common (e.g., Okutani, 2000; Redfern, 2001), photos of live animals are particularly abundant in the work under consideration, and include highly obscure and rarely shown groups (*Casiella abylensis* Gofas, 1987: Cerithiidae; Cerithiopsidae, Triphoridae, Velutinidae, seven (!) species of *Buncina*, Galeommatidae). Some drawings of live animals complement the overall work (e.g., Scissurellidae, Tornidae, Cystiscidae).

The work is rounded out with a 12-page glossary of terms, 25 pages of locality data for the specimens shown, and 12 pages of taxonomic index; there is no comprehensive listing of literature cited.

The most relevant comparison of Gofas et al. is with Cossignani and Adrovini (2011). Both are comprehensive treatments of all classes, rich in high quality illustrations. The text in Gofas et al. is in Spanish only but is much more comprehensive than the Italian/English sections in Cossignani and Adrovini. Gofas et al. includes all mollusks, without any omissions, while Cossignani and Adrovini is comprehensive for the shelled mollusks (e.g., Pendromidae), only presents a selection of cephalopods and opisthobranchs, and does not contain any of the worm mollusks. The illustrations in both volumes are excellent; Cossignani and Adrovini shines in showing about twice to three times as many specimens per species than Gofas et al. The latter, however excel with flawless and crisp printing, complementary light and electron microscopy images, as well as abundant photographs of live animals.

Considering the purpose of an identification manual (as opposed to a faunal monograph or a taxonomic revision), Gofas et al. reach that goal easily. Some decisions with respect to the classification may surprise some

readers. There are no taxonomic categories between class and family, and although the recent reclassification of the turrids is discussed, all Conoidea are treated under a single family heading "Conidae y afines" [Conidae and similar]. Given the long history of taxonomy in the European-Mediterranaen region with a plethora of taxa introduced, indications of species-level synonyms would have been highly desirable. The main drawback of this volume is possibly the Spanish language. For people who know any other Romance language, it does not pose any significant difficulties. Lucas Cervera Currado (pers. comm.) informed me that an English version is under consideration. Although the work is listed on the publisher's website, it is not available through them (P. Valentich-Scott, pers. comm.); it is however expected to be listed shortly by the usual outlets (e.g., ConchBooks, Mal de Mer).

The editors and authors of the *Moluscos Marinos de Andalucia* can be congratulated for a job well done. For people interested in the European malacofauna this is a must-have item, and is worthy of serious consideration for everybody else.

LITERATURE CITED

Ardovini, R. and T. Cossignani. 1999. Atlante delle Conchiglie de Profundità de Mediterraneo. L'Informatore Piceno, Aneona, 111 pp.

Bucquoy, E., P. Dautzenberg, and G. Dollfus. 1882–1886. Les Mollusques Marins du Roussillon. J.-B. Baillière & Fils, Paris, 570 pp., 66 pls.

Cossignani, T. and R. Ardovini. 2011. Malacologia Mediterranea. L'Informatore Piceno, Ancona. 536 pp.

D'Angelo G. and S. Garguillo. 1978. Guida Alle Conchiglie Mediterranee. Fabbri Editori, Milano, 224 pp.

Giannuzzi-Savelli, R., F. Pusateri, A. Palmeri, and C. Ebreo. 1994. Atlas of Mediterranean Sea Shells, Volume 1. La Conchiglia, Rome, 125 pp.

Høisaeter, T. and D. L. Geiger. 2011. Species of *Anatoma* (Gastropoda: Anatomidae) in Norwegian and adjacent waters, with the description of two new species. The Nautilus 125: 89–112.

Nordsieck, F. 1968. Die europäischen Meeres-Gehäuseschnecken (Prosobranchia) vom Eismeer bis Kapveden und Mittelmeer. Gustav Fischer Verlag, Stuttgart, 273 pp.

Nordsieck, F. 1969. Die europäischen Meeresmuscheln (Bivalvia) vom Eismeer bis Kapveden, Mittelmeer und Schwarzes Meer. Gustav Fischer Verlag, Stuttgart, 256 pp.

Nordsieck, F. 1972. Die europäischen Meeresschnecken (Opisthobranchia mit Pyramidellidae, Rissoacae). Gustav Fischer Verlag, Stuttgart, 327 pp.

Nordsieck, F. 1982. Die europäischen Meeresgehäuseschnecken, 2. Auflage. Gustav Fischer, Stuttgart, 539 pp.

Okutani, T. (ed.). 2000. Marine Mollusks in Japan. Tokai University Press, Tokyo, 1173 pp.

Poppe, G. T. and Y. Goto. 1991. European Seashells, Vol. I. Christa Hemmen, Wiesbaden, 352 pp.

Poppe, G. T. and Y. Goto. 1993. European Seashells, Vol. II. Christa Hemmen, Wiesbaden, 221 pp.

Redfern, C. 2001. Bahamian Seashells. Bahamianseashells .com, Boca Raton, Florida, 280 pp.

Schmekel, L. and A. Portman. 1982. Opisthobranchia des Mittelmeeres. Nudibranchia und Saccoglossa. Springer, Berlin, 410 pp.

Weinkauff, H.C. 1867. Die Conchylien des Mittelmeeres, ihre geographische und geologische Verbreitung. Band I Mollusca acephala. Theodor Fischer, Cassel, 301 pp.
Weinkauff, H.C. 1868. Die Conchylien des Mittelmeeres, ihre geographische und geologische Verbreitung. Band II Mollusca cephala. Theodor Fischer, Cassel, 512 pp.

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Notice

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ABSTRACT

In this study we conducted a survey of the diversity and abundance of species of the genus *Conus* over two macrohabitats in the eastern rim of the Bismarck Archipelago at the northern tip of New Ireland province of Papua New Guinea. The main aim was to set a baseline for the future use of *Conus* species as a biodiversity indicator to monitor human impact and conservation efforts in this region. We observed 422 live cone snails on 10 reefs covering 30 different species, with an overall diversity index of 0.924. The two habitats displayed a 74% proportional similarity with an average *Conus* density of 24 ± 9/ha (x ± SD, total sampled surface area: ~0.652 km^2). *Conus flavidus*, *C. miles*, *C. sanguinolentus*, *C. distans* and *C. litteratus* were the five most abundant species. Night sampling at marine-protected Lissenung Island highlighted substantial differences between day and night observations. Sampling at 30 m depth confirmed the presence of the recently identified *C. moncuri* in this area. Overall, genus *Conus* was strongly present in all of the sampled sites and represents a good low-cost indicator for long-term studies of human impact and facile comparison of the health of similar, but geographically distant ecosystems.

Additional keywords: *Conus*, cone snail, biodiversity indicator, Papua New Guinea, New Ireland, abundance

INTRODUCTION

Conus is the largest known genus of marine invertebrates, with over 500 extant species, although the total described number of species may be much higher with more than 2,000 species catalogued between 1758–1998 (Filmer, 2001). *Conus* belongs to the superfamily Conacea (suborder Toxoglossa), collectively referred to as the toxoglossate gastropods (Taylor et al., 1993; Olivera, 2002). Cone snails are found in tropical marine environments and are particularly prominent around coral reefs and other shallow-water tropical marine habitats (Kohn, 1967; Kohn, 1968; Kohn, 1971; Kohn and Nybakken, 1975; Heck and Wetstone, 1977). In particular, the "Coral Triangle" in the central Indo-Pacific region, encompassing parts of Indonesia, Papua New Guinea (PNG), Malaysia and the Philippines, is well known for its rich marine biodiversity and considered a hot spot for *Conus* with more than 30 different species observed to co-occur on a single reef (Kohn, 2001). At the same time, it is an area that is severely threatened by human impact due to over-fishing, pollution and expanding populations (Allen and Werner, 2002). Highly prized by collectors, the shell of cone snails comes in a variety of patterns and colors, making them attractive and valuable items. Yet, the decorative shell of the cone snail provides no clue to its reputation as one of the most venomous creatures on the planet (Nelson, 2004). Indeed, all *Conus* species possess an efficient venom delivery system used for prey capture and defense (Olivera, 2002). The venom is a complex mixture containing hundreds of highly structured biologically active peptides (Davis et al., 2009), which functionally modulate various ion channels to induce paralysis (Han et al., 2008; Lewis, 2009). Only a small number (< 100) of these venom peptides have been characterized so far, still these peptides already afforded a drug of proven clinical utility (Prialt, isolated from *C. magus* (Miljanich, 2004)), several pre-clinical leads for CNS disorders and many valuable tools for neuroscientists, in particular for the treatment and understanding of pain. It should therefore be of high interest to increase conservation efforts to preserve this remarkable pharmacopeia.

Hence, we set out to investigate the diversity and abundance of the genus *Conus* at the northern tip of New Ireland province of Papua New Guinea (Figure 1),

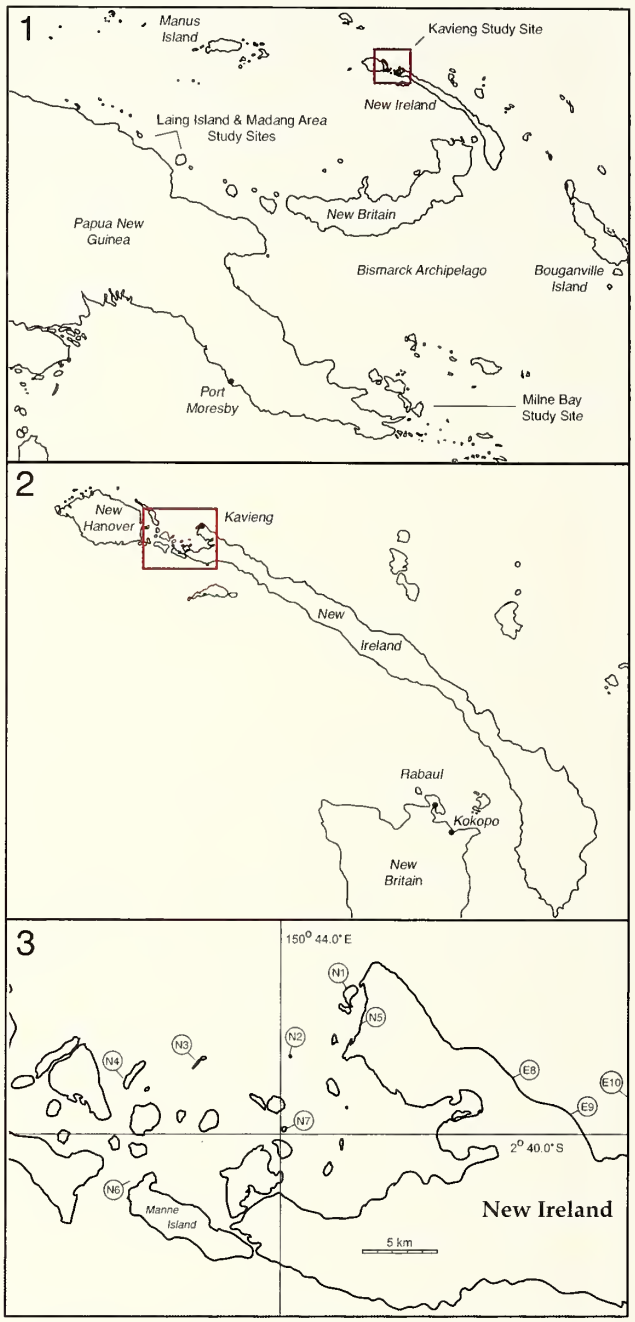
to increase local understanding of the benefits of marine protected zones, to train local research staff, and to assess if cone snails can be used as a local biodiversity indicator for long-term monitoring of human impact and conservation efforts in this region.

Mollusks in general are one of few phyla routinely used as biomarkers in marine biodiversity surveys and are considered an appropriate indicator group for the rapid assessment of biodiversity of organisms inhabiting coral reefs (Wells, 1998; Wells and Kinch, 2003). Although *Conus* abundance and diversity are inversely proportional to living coral cover on Indo-Pacific reefs (Kohn, 1983), its presence and diversity adjacent to reefs relates to a healthy ecosystem since they are predators of many other animals (worms, mollusks, and fish). Additionally, species identification is unproblematic due to the long interest of numerous malacologists and shell collectors providing quality information on molluscan shell patterns surpassed probably only by that on fish. Three earlier studies conducted in PNG (Figure 1), two in 1997 and 2000 in Milne Bay province (Wells, 1998; Wells and Kinch, 2003), and another one in 1997 in the Madang area (Kohn, 2001) already reported high diversity of *Conus*, observing 66 different species in the Milne Bay area and 45 in the Madang area. The survey described in this publication observed 422 live *Conus* specimens of 30 different species in the Kavieng area at the northern tip of New Ireland province of PNG (Figures 1–3). This strong presence and diversity of *Conus* in this region in combination with its correlation to ecosystem health (Veron, 2000; Roberts et al., 2002) warrants its use as an indicator for long-term monitoring of human impact in this region.

MATERIALS AND METHODS

Study Sites: Ten different reefs were investigated between the 8–14 July 2010 for cone snail abundance and diversity in Papua New Guinea (Figure 3). The sites selected for this study were located at the northern tip of New Ireland (Tok Pisin: Niu Ailan, approximately 2°37′ S, 150°45′ E) province, a long and narrow island (approximately 8650 km^2) situated on the eastern rim of the Bismarck Archipelago. Two seasons are experienced annually in this area: dry southeasterly trade winds blow almost continuously between May and August, and the northwesterly, rain-bearing monsoon prevails from December to March. The months between April and September are generally recommended for such expeditions due to aerial reef exposure at low tides (0.2–0.6 m), which significantly facilitates sampling. The water temperature does not vary much over the year, ranging from 28–30° C.

Different marine environments in the area surrounding Kavieng were investigated at depths to 30 m. Small islands on barrier reef and the rocky island of New Ireland were surrounded by multiple reef types, including coral-rich fringing reefs, reef shelves, patch reefs, sea grass and sandy-bottom reef flats (Table 1 and

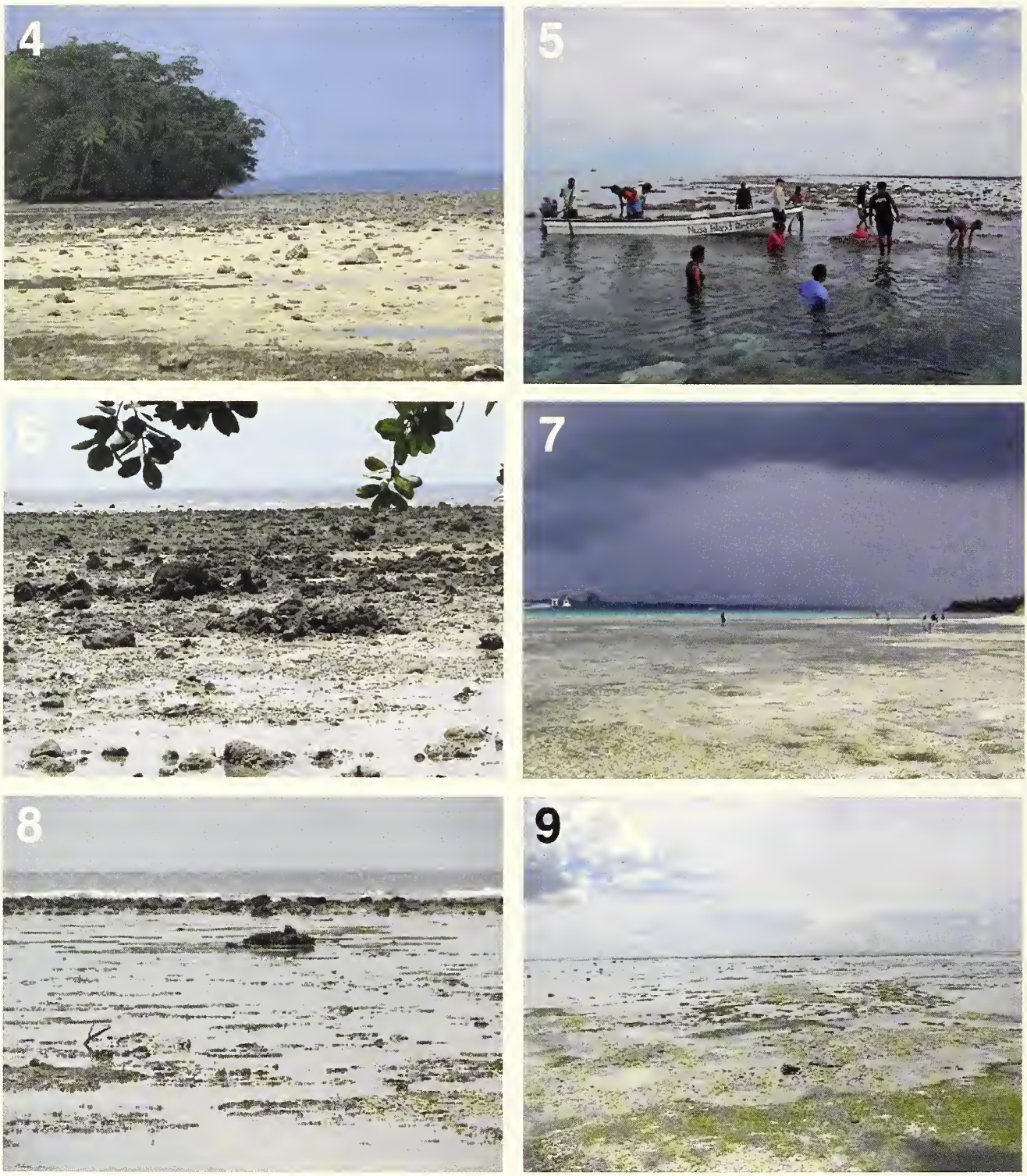


Figures 1–3. Location of study sites in the Bismarck Archipelago / Papua New Guinea. **1.** Geographical overview of the three study sites: Milne Bay area (1997, 2000), the Laing Island and Madang area (1997), and the Kavieng area (2010, this paper). **2.** Close-up on New Ireland, showing Kavieng area, which is situated at the northern tip of New Ireland Province. **3.** Close-up on the Kavieng area, displaying the reef locations that were studied. The lagoon-like sites were labeled N1–N7 and the outer reef sites on the East Coast of New Ireland were labeled E8–E10.

Table 1. Description of the individual study sites including GPS coordinates, measured sample area, description of habitat, sampling time, high and low tides, number of people collecting per site and calculated sampling efficiency based on surface area and sampling effort.

#	Site name	GPS	Area m^2	Habitat	Time	Tides	Depth	People	Efficiency
A	**Northern Island platform reefs**								
N1	Big Nusa Island	02° 34.437′ S, 150° 46.458′ E 02° 34.131′ S, 150° 47.066′ E	106 000	Fringing reef, reef flat, boulders, coral rubble, sand-filled depressions	180 min 09.00–12.00	09.00: 0.35m 16.21: 0.97m	0–5 m	9	25%
N2	Edmagou Island	02° 36.999′ S, 150° 44.193′ E	42 000	Barrier reef, patch reef, coral-rich, rocky limestone reef	45 min 09.30–10.15	09.27: 0.30m 16.45: 0.95m	0–5 m	15	27%
N3	Nusalaman Island	02° 37.380′ S, 150° 40.280′ E	123 000	Fringing reef, sandy-bottom	145 min 10.35–13.00	09.27: 0.30m 16.45: 0.95m	0–5 m	15	29%
N4	Limus Island	02° 38.041′ S, 150° 37.460′ E	92 000	Fringing reef, patch reef, sandy-bottom	90 min 14.30–16.00	09.27: 0.30m 16.45: 0.95m	0–5 m	15	24%
N5	Fisheries Jetty	02° 35.444′ S, 150° 47.255′ E	30 000	Lagoon, sandy-bottom, seagrass	150 min 9.00–11.00	09.56: 0.29m 17.10: 0.95m	0–5 m	3	25%
N6	Albatross Passage	02° 36.659′ S, 150° 42.577′ E	20 000	Barrier reef, reef shelf, patch reef, sandy-bottom	60 min 10.00–11.00	10.28: 0.33m 17.35: 0.96m	5–30 m	3	15%
N7	Lissenung Island	02° 39.910′ S, 150° 43.974′ E 02° 39.883′ S, 150° 44.086′ E	40 000	Fringing reef, coral rubble, seagrass, sandy-bottom	60 min 20.45–21.45	10.28: 0.33m 17.35: 0.96m	5–15 m	6	15%
B	**East Coast fringing reefs**								
E8	Kaselok 1 Reef	02° 37.405′ S, 150° 53.171′ E	87 000	Fringing reef, rocks, coral rubble	105 min 09.30–11.15	09.56: 0.29m 17.10: 0.95m	0–5 m	16	32%
E9	Kaselok 2 Reef	02° 38.780′ S, 150° 55.093′ E	61 000	Fringing reef, rocks, coral rubble, sandy canyons	70 min 11.50–13.00	09.56: 0.29m 17.10: 0.95m	0–5 m	16	31%
E10	Fanalawa Reef	02° 51.759′ S, 151° 12.313′ E	51 000	Fringing reef, big rocks, sandy patches, canyons	60 min 14.30–15.30	09.56: 0.29m 17.10: 0.95m	0–5 m	16	31%

Figures 4–9 Figure 3). The inner reefs and reef crests were exposed during low tides and explored on foot during these times. The outer reefs and lagoons were explored through a combination of free-diving and SCUBA. The explored sites were grouped into two general zones, each incorporating multiple reef environments and microhabitats. The Northern Islands (NI) group consisted of an island chain on the western side of New Ireland connected by a barrier reef, extending south from Kavieng to the western coast of Manus Island (Figure 3). This area displayed a rich environmental heterogeneity including barrier reef, fringing reef, reef shelves, patch reefs, lagoons and subtidal reef flats. The outer islands, in particular Nusa Island (site N1 in Figure 3), contained many boulders, sand-filled depressions and few corals, a preferred habitat for many cone snail species. A few islands on the inner (eastern side) barrier reef were also explored including a marine protected zone at Lissenung Island (Site N7 in Figure 3). This inner region was made up of an intra-lagoon patch reef and reef flat environments. The southern end of a barrier reef terminated in a reef wall between two small islands in an area called Albatross Passage (N6), which was also explored. The NI region generally exhibited slow



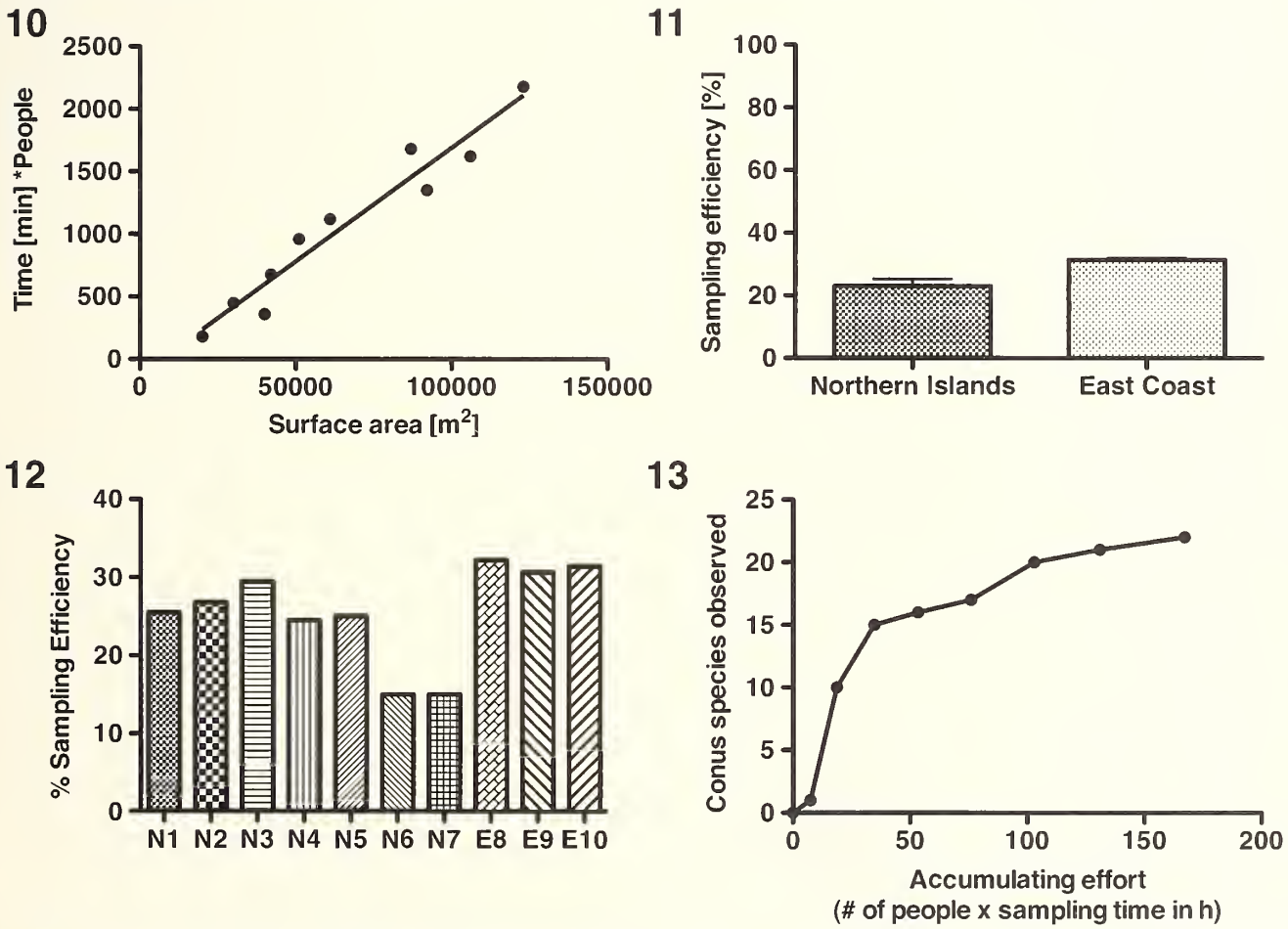
Figures 4–9. Habitats and reef morphologies of the study sites. **4–7.** Northern Islands Region. **4.** Large subtidal reef flat of Nusa Island (N1). **5.** Rocky and coral-rich patch reef of Edmagon Island (N2). **6.** Rocky limestone reef flat of Limus Island (N4). **7.** Shallow sandy lagoon of the southern part of Nusa Island (N1). **8–9.** East Coast Region. Typical fringing reef environment found in the EC region consisting of boulder and coral-rubble rich inner reef flats, limestone benches and coral-rich canyons in the outer reef.

surface currents with low wave energy on reef edges, as it was located on or inside of a protective barrier reef.

The second zone incorporated the northern tip of the East Coast (EC) of New Ireland and exhibited less environmental heterogeneity than the N1 region. The EC region was composed of fringing reef extending to a reef shelf into deep, open water and was explored from Kaselok to Fangalava (Figure 3). This region experiences strong surface currents at the reef shelf as well as increased wave energy where the fringing reef drops off as a reef shelf, due to the exposed and unprotected nature of the reef facing the open ocean.

Sampling Methods: Sampling was conducted at low tides by a combination of walking on aerially exposed reefs and snorkeling at the edges of the exposed reef platforms and lagoons at depths of 0–5 m. Boulders were overturned and examined for live snails, trails in sand were followed up and coral rubble was examined. Site N6 was sampled at a depth of 5–30 m and site N7 at a depth of 5–15 m by SCUBA. Identification of the species was carried out using the shell book 'Manual of the living Conidae' (Rockel et al., 1995) either on site or at a later stage, when the periostracum was removed from collected shellswith bleach. *Conus moncuri* was identified *via* correspondence with the cone snail expert R. M. Filmer. Only live cone snails were recorded. Most observations had to be conducted during the daytime (Table 1) since nocturnal observations were not feasible, with the exception of N7, where necessary facilities were in place.

The number of people sampling varied at individual sites (Table 1) due to the educational training program requirements between the University of Queensland and the National Fisheries Authority. Time sampling was preferred, as initial attempts to use spatial transects indicated a low *Conus* density, which would result in an inefficient use of time within the intertidal zones. Hence only time-relative densities were used for analysis. Sampling effort at the individual sites correlated well with the estimated surface area (Figure 10, $r^2 = 0.9389$, using GPS coordinates and a surface measurement software www.freemaptools.com/area-calculator.htm). The method had the distinct advantage of time efficiency in the intertidal zone, which allowed observers to cover large reef areas within reasonable time limits.



Figures 10–13. **10** Linear correlation of measured surface area and sampling effort ($r^2 = 0.9389$). **11** and **12** Calculated macrohabitat-specific (**11**) and site-specific (**12**) sampling efficiencies.. **13** Correlation of live *Conus* species observed during the day with accumulation of effort.

In total, 16 hours were spent sampling over an estimated total area of 0.652 km^2. Considering an average of 1000 m^2 that a person could sample per hour (based on the first three sites N1–N3), an overall sampling efficiency of 26% was observed, reflecting factors such as reef morphologies, accessibility, *Conus* habitat (boulders, coral rubble, etc.) and type of sampling (reef walking, snorkeling, diving). The sampling efficiency was calculated using the following formula: E [%] = {sampling time [h] * number of people} * 1000 [m^2 h^{-1}] *100 [%] / surface area [m^2]. The EC sites were generally more accessible than the NI sites, mainly due to reef morphology, which correlated well with the individual sampling efficiencies observed per site (Figure 11 and 12). Increasing collecting experience might also have contributed to the higher efficiencies at the EC sites, which were sampled last.

Data Analyses: The study sites were marked using a handheld Garmin 60CXS GPS system and the sampled surface areas were measured using GPS guided surface area calculating software available online (www.freemaptools.com/area-calculator.htm). All GPS coordinates are in the world geodetic system 1984 format. *Conus* species abundance was determined by measure of effort, based on the absolute numbers of species observed divided by the number of people sampling and by the sampling time in hours. *Conus* species diversity was determined using the Simpson's Index $D = 1-\sum(n/N)^2$, where n is the total number of organisms of a particular species and N is the total number of organisms of all species. The Simpson's Index was used instead of the Shannon-Weaver Index because it is less sensitive to sample size and therefore more representative for diversity when densities are low (Kohn and Nybakken, 1975; Routledge, 1979). The proportional similarity of the two habitats was carried out using the Sørensen Index QS=2C/(A+B), where *A* and *B* are the number of species in NI and EC, respectively, and *C* is the number of species shared by both habitats. The time-related *Conus* species densities were calculated based on the number

Table 2. Absolute numbers of live cone snails observed per site.

Site	*Conus* species	#	Site	*Conus* species	#	Site	*Conus* species	#
Northern Islands Area								
N1	*flavidus*	35	**N2**	*distans*	10	**N3**	*distans*	19
	miles	21		*miles*	9		*miles*	9
	sanguinolentus	13		*litteratus*	3		*flavidus*	8
	ebraeus	11		*canonicus*	2		*frigidus*	4
	litteratus	2		*imperialis*	1		*sanguinolentus*	2
	distans	2		*virgo*	1		*emaciatus*	1
	musicus	1		*frigidus*	1		*leopardus*	1
	leopardus	1		*chaldaeus*	1		*lividus*	1
	chaldaeus	1		*flavidus*	1		*rattus*	1
	catus	1		*lividus*	1		*textile*	1
N4	*flavidus*	10	**N5**	*litteratus*	11	**N7**	*marmoreus*	6
	frigidus	7					*leopardus*	6
	miles	4					*virgo*	4
	sanguinolentus	2	**N6**	*moncuri*	1		*terebra*	3
	canonicus	1					*striatus*	2
	lividus	1					*textile*	2
	emaciatus	1					*vexillum*	2
							arenatus	1
							aulicus	1
							geographus	1
East Coast Area								
E8	*miles*	29	**E9**	*flavidus*	9	**E10**	*miliaris*	7
	flavidus	15		*sanguinolentus*	8		*sanguinolentus*	7
	sanguinolentus	15		*miles*	7		*lividus*	6
	lividus	9		*miliaris*	8		*frigidus*	6
	frigidus	7		*lividus*	6		*flavidus*	6
	distans	9		*frigidus*	6		*rattus*	4
	miliaris	4		*rattus*	3		*tulipa*	3
	rattus	2		*tulipa*	1		*ebraeus*	3
	imperialis	1		*chaldaeus*	1		*distans*	2
	virgo	1		*striolatus*	1		*canonicus*	1
	leopardus	1					*miles*	1
	coronatus	1					*imperialis*	1

of *Conus* species individuals found per person per hour at each site. The space-related densities were derived from the time-related densities considering ~1000 m^2 that a person could sample per hour (based on the first three sites N1–N3) including the sampling efficiency (% of actual sampled surface area) (Figure 17).

RESULTS

In total, 422 specimens of 30 different species were observed, out of which 26 species were found in the NI region and 17 in the EC region (Table 2). Thirteen *Conus* species (*canonicus, chaldaeus, distans, ebraeus, flavidus, frigidus, imperialis, leopardus, lividus, miles, rattus, sanguinolentus,* and *virgo*) were common in both habitats, five *Conus* species (*catus, emaciatus, musicus, litteratus,* and *textile*) were only found in the NI region, four *Conus* species (*coronatus, miliaris, striolatus,* and *tulipa*) only in the EC region and seven *Conus* species (*arenatus, aulicus, geographus, marmoreus, striatus, terebra,* and *vexillum*) were only found at night at the protected marine zone Lissenung (N7) (Figure 14). *Conus moncuri,* which has so far not been observed in the PNG area, was found at a divide in the barrier reef, called the Albatross Passage (N6) at a depth of 30 m (Figure 3). The majority of species found was worm hunters (21), followed by fish hunters (5) and mollusk hunters (4) (Figure 15).

The Simpson's Diversity Index for the whole region was 0.924, for the NI region (N1–N5) 0.858 and for the EC region 0.882. N6 and N7 were analyzed separately due to site and sampling differences (Table 1). However, both sites were located within the NI area and the diversity index including N6 and N7 was calculated to be 0.918. The Simpson's Diversity Indices for each individual site are listed in Figure 16 with site EC10 having the highest diversity with an index of 0.888. The Diversity Index of the protected marine zone Lissenung (N7) was 0.857. In comparison, the Sørensen Index showed a 74% species similarity between the two macrohabitats (N1–N5 vs. EC8–EC10), with a 62% species similarity observed when the sites N6 and N7 were included.

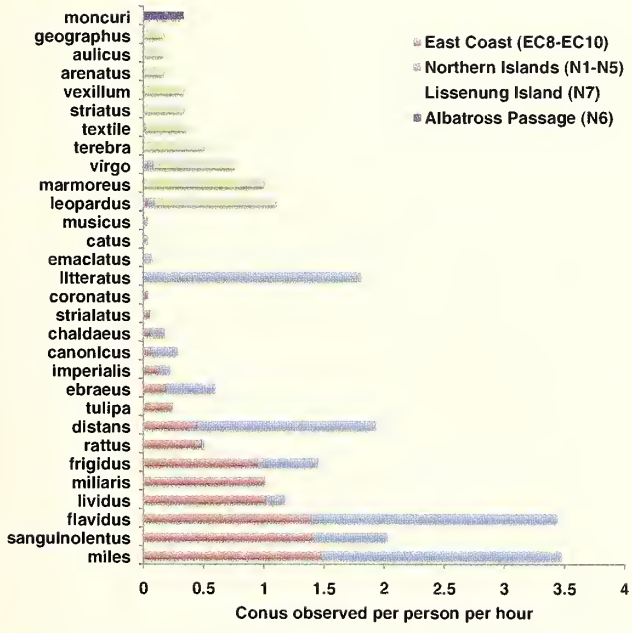


Figure 14. *Conus* species abundance of Northern Islands (blue), East Coast (red), Lissenung Island (green) and Albatross Passage (purple).

The total number of each species found in each macrohabitat is listed in Figure 15. The five most abundant species across the regions studied were *C. miles, C. flavidus, C. sanguinolentus, C. distans,* and *C. litteratus,* in the EC region *C. miles, C. sanguinolentus, C. flavidus, C. lividus,* and *C. miliaris,* and in the NI region *C. flavidus, C. miles, C. litteratus, C. distans, C. leopardus* and *C. marmoreus,* ranked by their abundance respectively (Figure 14). The EC area showed slightly higher abundance with 3.0 ± 0.3 (x ± SD) cone snails per 1000 m^2 (or per hour per person) than the NI area (N1–N5) with 2.0 ± 0.9 (x ± SD) (Figure 17). This relates to an overall mean density of 2.4 ± 0.9 (x ± SD) *Conus* per 1000 m^2. The curve of newly identified species observed with increasing sampling effort tends to level off indicating that the species found in the Kavieng area represent an adequate reflection of the entire community, excluding diurnally buried species as well as cone snails found at depths > 5 m (Figure 13).

DISCUSSION

Many factors make the genus *Conus* an important biodiversity indicator, particularly for ecosystems adjacent to reefs where corals are generally absent or scarce (e.g.: mud, sand, and rubble bottoms). These factors include high species diversity, its global presence in tropical waters, well-established taxonomy, ecological and economic importance, its survival over millions of years and its strong correlation to local fish and coral biodiversity (Veron, 2000; Roberts et al., 2002). 422 live cone snails encompassing 30 different species were observed in the two main macrohabitats, the Northern Island (NI, including fringing reef, barrier reef, platform reefs and lagoons) and the East Coast (EC, fringing reefs), over a total area of ~0.652 km^2. These numbers warrant enough abundance and diversity to measure ecosystem health and address human impact if assessed on a regular basis. 26 species were found in the NI region and 17 species on the fringing reefs of the EC area. The two macrohabitats displayed a 74% proportional species similarity with 13 species present in both regions (Figure 14). Of these 13, *C. flavidus, C. miles, C. sanguinolentus, C. distans,* and *C. frigidus* were the five most abundant. By contrast, *C. miliaris, C. tulipa, C. striolatus,* and *C. coronatus* were confined to the EC habitat, while *C. litteratus, C. emaciatus, C. catus, C. musicus,* and *C. textile* seemed to prefer the NI region. The NI region had a richer display

Conus species	Prey	#	*Conus* species	Prey	#	*Conus* species	Prey	#
orenatus	warm	1	*frigidus*	warm	48	*musicus*	worm	1
oulicus	mollusc	1	*geogrophus*	fish	1	*rottus*	worm	10
cononicus	mollusc	4	*imperiolis*	warm	3	*sanguinolentus*	worm	64
catus	fish	1	*leopordus*	warm	9	*striotus*	fish	2
chaldaeus	warm	3	*litterotus*	warm	16	*striolatus*	fish	1
coronatus	warm	1	*lividus*	warm	49	*terebra*	warm	3
distons	warm	42	*mormoreus*	mollusc	6	*textile*	mollusc	3
ebraeus	worm	14	*miles*	warm	96	*tulipa*	fish	4
emociatus	warm	2	*milioris*	warm	20	*vexillum*	warm	2
flovidus	warm	101	*moncuri*	warm	1	*virga*	warm	6
	NI Species	26		EC Species	17		Species total	30
	NI Individuals	231		EC Individuals	191		Individuals total	422

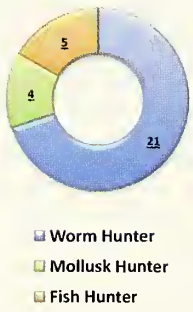
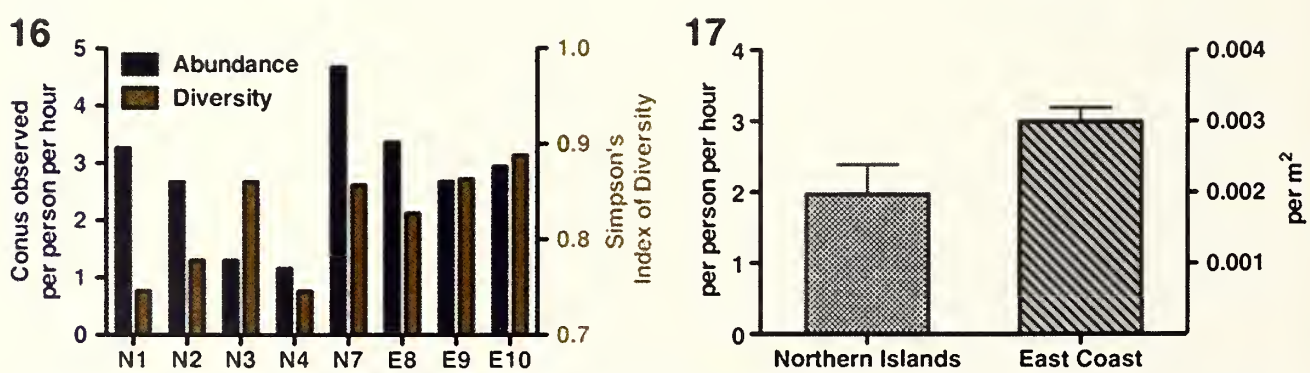


Figure 15. Number of *Conus* species and individuals observed including their type of prey.

of environmental heterogeneity compared to the EC region including multiple reef types such as barrier reef, patch reef, fringing reef and sandy-bottom reef flats. These different microhabitats in turn influence *Conus* presence at the studied sites: *Conus litteratus* and *marmoreus*, for example, were not only confined to the NI region, but more particularly to sandy bottoms devoid of corals and strong currents. *Conus flavidus*, *sanguinolentus*, and *ebraeus* were strongly present at site N1, which contained a large subtidal reef flat with many boulders and sand-filled depression (Figure 4), yet both species were absent at neighboring site N2, which was a coral-rich rocky limestone reef (Figure 5).

Many cone snails are nocturnal predators and are hiding under rocks/coral rubble or are buried in sand during the day (Terlau and Olivera, 2004). Lissenung Island (N7) had the facilities necessary (dive resort, high-energy light sources, trained dive staff and local guides) to conduct night sampling, which allowed us to observe some of the nocturnal species. Night sampling resulted in observation of 7 out of 10 *Conus* species (*marmoreus*, *terebra*, *striatus*, *vexillum*, *arenatus*, *aulicus*, and *geographus*) that were not found at any of the other sites (Figure 14) strongly suggesting that night sampling should be incorporated in future surveys. Lissenung Island was also the only protected marine zone in this area (no fishing or shell collecting), which could have been another factor contributing to the high abundance and diversity observed at this site (Figure 16).

Two earlier studies reporting on *Conus* species diversity in PNG were part of the Rapid Marine Biodiversity Assessment conducted in 1997 and 2000 that covered the area of the Milne Bay Province, which encompasses the extreme southeastern tip of mainland Papua New Guinea and an extensive offshore area immediately eastward (Figure 1) (Wells, 1998; Wells and Kinch, 2003). They covered an area heavily dotted with islands and shoals in the Solomon Sea separating PNG from the neighboring Solomon Islands. The mollusk survey in 2000 included 28 different sites over a period of 11 days and to date represents the most thoroughly conducted assessment of *Conus* species diversity in this region. 66 different *Conus* species were observed with *C. miles* being the most abundant and widely distributed species in Milne Bay (15 out of 28 sites). From the 30 species observed in the Kavieng area, all but two *Conus* species (*C. striolatus*, *C. moncuri*) were also found in the Milne Bay survey. *Conus moncuri* is a relatively newly discovered species that has so far not been reported in PNG, although it has been observed in the Solomon Islands and the Philippines. Its described habitat is between 30 and 50 m depth, which might be the main reason for its rare spotting, as diving at these depths is still not very common for shell collectors.



Figures 16–17. **16.** Comparison of *Conus* species abundance and diversity per study site. The sites N5–6 were excluded because only a single species was observed at these sites. **17.** Cone snail density of the two macrohabitats, Northern Islands area (N1–N5) and East Coast area (E8–E10, mean ± S.E.).

The third study conducted in PNG in 1997 covered Laing Island and the Madang area (200 km apart, Figure 1) and observed 45 species, which correlated well with the species observed in this survey. Only *C. sanguinolentus* and *C. moncuri* were not observed, which is surprising, as *C. sanguinolentus* was one of the most abundant species in our study. *Conus miliaris* was the most abundant species in the Madang area, which was also highly abundant in the Kavieng area, although only confined to the EC fringing reef habitat. The preferred microhabitats for *C. miliaris* on Laing Island were limestone bench and coral rock, both of which were also found in abundance at all three EC sites. Differences in site selection (non-random selection to maximize *Conus* species diversity and density), sampled surface area (386 m^2 Laing Island and 3511 m^2 Madang), observation period (5 weeks), sampling methods (transects, quadrants, inclusion of dead shells) and data analysis do not allow quantitative comparison with our study, however observations such as 36 different *Conus* species co-occurring on single reef platforms and maximal densities of 3/m^2 were not observed in our survey. The studies were conducted more than a decade ago and it certainly would be of interest to see if this rich diversity and abundance has persisted in these areas.

Overall, *Conus* species are strongly present in the northern part of the province of New Ireland of Papua New Guinea, with 422 individuals of 30 different species observed. The local residents may easily report their observations, making *Conus* an attractive low cost biodiversity indicator for long-term monitoring of a wide region. Additionally, the global presence of the species of the genus enables facile comparison of similar, but geographically distant ecosystems. As expected, significant species differences were observed between day and night sampling recommending the inclusion of night sampling in future surveys. It is important that the staff conducting these surveys will receive appropriate training and gain experience, so that the sampling efficiency only reflects reef accessibility and morphology rather than sampling experience. The high abundance and diversity observed at the marine-protected zone at Lissenung Island shows promise that *Conus* species can be used to monitor and validate human conservation efforts in this region. This project should lead to regular assessments in this region, stimulate further studies in this field and initiate local involvement to preserve regional biodiversity and marine richness in Papua New Guinea.

ACKNOWLEDGMENTS

We would like to thank the people from the various communities in the Tigak islands and East Coast of mainland New Ireland for their understanding and allowing us to access their reef areas. Additionally, we thank the National Fishery Authority of PNG and Ailan Awareness Inc for the collaborative effort and in particular we thank all the individual people involved in this project, Dr. Thomas Durek, Dr. Lachlan Rash, Mr. Peter Minimulu, Mr. Casper Dako, Mr. Jacob Wani, Mr. Shaun Keane, Mr. Dietmar Amon, John and all the students that helped with the collection. The research leading to these results has received funding from the NHMRC Program Grant (569927) and from the *European Union* Seventh Framework Programme (*FP7/2007-2013*) under *grant agreement* n° [*254897*].

LITERATURE CITED

Allen, G.R. and T.B. Werner 2002. Coral reef fish assessment in the 'Coral Triangle' of Southeastern Asia. Environmental Biology of Fishes 65: 209–214.

Davis, J., A. Jones, and R.J. Lewis 2009. Remarkable inter- and intra-species complexity of conotoxins revealed by LC/MS. Peptides 30: 1222–1227.

Filmer, R.M. 2001. A Catalogue of Nomenclature and Taxonomy in the Living Conidae 1758–1998. Backhuys Publishers, Leiden, 388 pp.

Han, T.S., R.W. Teichert, B.M. Olivera, and G. Bulaj 2008. *Conus* venoms - a rich source of peptide-based therapeutics. Current Pharmaceutical Design 14: 2462–2479.

Heck, K.L.J. and G.S. Wetstone 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. Journal of Biogeography 4: 135–142.

Kohn, A.J. 1967. Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-West Pacific reef platforms. The American Naturalist 101(919): 251–259.

Kohn, A.J. 1968. Microhabitats, abundance and food of *Conus* on atoll reefs in the Maldive and Chagos Islands. Ecology 49: 1046–1062.

Kohn, A.J. 1971. Diversity, utilization of resources, and adaptive radiation in shallow-water marine invertebrates of tropical oceanic islands. Limnology and Oceanography 16: 332–348.

Kohn, A.J. 1983. Microhabitat factors affecting abundance and diversity of *Conus* on coral reefs. Oecologia 60: 293–301.

Kohn, A.J. 2001. Maximal species richness in *Conus*: diversity, diet and habitat on reefs of northeast Papua New Guinea. Coral Reef 20: 25–38.

Kohn, A.J. and J.W. Nybakken 1975. Ecology of *Conus* on eastern Indian Ocean fringing reefs: Diversity of species and resource utilization. Marine Biology 29: 211–234.

Lewis, R.J. 2009. Conotoxins: molecular and therapeutic targets. Progress in molecular and subcellular biology 46: 45–65.

Miljanich, G.P. 2004. Ziconotide: neuronal calcium channel blocker for treating severe chronic pain. Current Medicinal Chemistry 11(23): 3029–3040.

Nelson, L. 2004. Venomous snails: one slip, and you're dead. Nature 429(6994): 798–799.

Olivera, B.M. 2002. *Conus* venom peptides: reflections from the biology of clades and species. Annual review of Ecology, Evolution, and Systematics 33: 25–42.

Roberts, C.M., C.J. McClean, J.E.N. Veron, J.P. Hawkins, G.R. Allen, D.E. McAllister, C.G. Mittermeier, F.W. Schueler, M. Spalding, F. Wells, C. Vynne, and T.B. Werner 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science (Washington, DC, U. S.) 295 (5558): 1280–1284.

Rockel, D., W. Korn and A.J. Kohn 1995. Manual of the Living Conidae. Verlag Christa Hemmen, Hackenheim, Germany.

Routledge, R.D. 1979. Diversity indices: Which ones are admissible? Journal of Theoretical Biology 76: 503–515.

Taylor, J.D., Y.I. Kantor, and A.V. Sysoev 1993. Foregut anatomy, feeding mechanisms, relationships and classification of Conoidea (Toxoglossa) (Gastropoda). Bulletin of the Natural History Museum 59: 125–169.

Terlau, H. and B.M. Olivera 2004. *Conus* venoms: a rich source of novel ion channel-targeted peptides. Physiological Reviews 84: 41–68.

Veron, J.E.N. 2000. Corals of the World. Australian Institute of Marine Science, Townsville.

Wells, F.E. 1998. Marine Molluscs of Milne Bay Province, Papua New Guinea. In: Werner, T.B. and Allen, G.R. (eds) A rapid biodiversity assessment of the coral reefs of Milne Bay Province, Papua New Guinea. Conservation International, Washington, DC, pp. 35–38.

Wells, F.E. and J.P. Kinch 2003. Molluscs of Milne Bay Province, Papua New Guinea. In: Allen, G.R., Kinch, J.P., McKenna, S.A. and Seeto, P. (Eds). A rapid marine biodiversity assessment of Milne Bay Province, Papua New Guinea—Survey II (2000). Conservation International, Washington, DC, USA: 39–45.

A new genus and two new species of deep-sea gastropods (Gastropoda: Vetigastropoda: Gazidae)

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ABSTRACT

A new genus and two new species of deep-sea vetigastropod gastropods extend knowledge of the unique shell morphology, radula, anatomy, ecology, and distribution of a family group of undetermined relationship to other vetigastropods. *Anomphalogaza moluccensis* new genus and new species is the first record of the family in the Indonesian biogeographic realm of Wallacea. *Callogaza colmani* new species is the first record of the family group from the Australian Plate. Determinate growth in all known gazid species is expressed in a pronounced thickening and reflection of the final lip along with a descending suture. In the umbilicate species, determinate growth is also marked by formation of a thin reflected callus that partially or fully isolates a hollow umbilical chamber. Unique features of the Gazid radula include extremely elongated marginal teeth with strongly serrate shafts and an unusual pattern of integration in which rows of marginal tooth bases and cusps are aligned in separate rows of raehidian and lateral teeth. Distinctive anatomical features include expanded oral surface of the snout, antero-lateral extensions of the foot, and an enlarged hindgut. Numerous repaired breakages of delicate gazid shells prior to formation of the terminal lip suggest high predation pressure. Occurrences in regions of methane and sulfide seepage suggest that these relatively large deposit-feeding gastropods are nutritionally linked with unconventional carbon sources.

Original description of the family group as a tribe within Margaritinae Thiele, 1924 was based on analysis of morphological features. Subsequent molecular sequence data have shown that Margaritinae is not monophyletic, and some deep-water species described under *Margarites* Gray, 1847 may be more closely related to the gazid species described herein. Because classification of vetigastropod family group taxa is currently in a state of flux, this treatment abstains from traditional ranked classification and uses the family-group ending "-idae" in a provisional sense until complete phylogenies are available.

Additional keywords: bathyal, chemosynthesis, methane, sulfide, cold seep, Molucca Sea, Australia, deposit feeding

INTRODUCTION

Morphological support for monophyletic vetigastropod groups, including monophyletic Turbinidae and Trochidae (Hickman and McLean, 1990; Hickman, 1996, 1998) is in increasing conflict with the results of more recent molecular analyses (e.g., Geiger and Thacker, 2005; Yoon and Kim, 2005; Williams and Ozawa, 2006; Kano, 2008; Williams et al., 2008, 2010). Although monophyly of some of the morphologically based subfamilies and tribes is well supported by new genetic data, there have been some major realignments of their relationships to one another. New morphological and/or molecular data have led to a revised working classification (Bouchet and Rocroi, 2005) and redefinitions of Trochidae, Turbinidae, and Trochoidea (Williams et al., 2008).

Some of the most interesting realignments are among higher taxa restricted to habitats in the deep sea (>200 meters). Recurring features that appear to be convergent in deep-water vetigastropods include minute shell size (<5 mm), reduced shell thickness and visibility of nacre (tabular aragonite) through a thin exterior layer, extreme thinning or putative loss of nacre, secondary loss of coiling resulting in a limpet shell form, enlargement of the hindgut associated with deposit feeding, elaboration of structures for sperm transfer and sperm storage, and, in some cases, hermaphroditism.

Examples of hypothesized molecular unmasking of convergence include the recognition of two discrete clades of minute slit-shells formerly united under Scissurellidae (Geiger and Thacker, 2005) and recognition of a close relationship among minute shells of seguenziiform taxa, large- and small-shelled deep-sea trochiform taxa, and a number of minute skeneiform taxa (Kano, 2008). Taxon sampling for molecular phylogenetic analysis is still problematic and difficult for the many deep-sea taxa that are known only from shells and occasional formalin fixed specimens in wet collections.

A major gap in sampling is that of the deep-sea family-group Gazidae Hickman and Mclean, 1990. Eight species in two genera, *Gaza* Watson, 1879, and *Callogaza* Dall, 1891, have many shared features (Hickman and McLean, 1990) that unite them phylogenetically (Hickman, 1996, 1998). These include shared character states for

38 of 40 radular characters (Hickman, 1996). However, the original placement of gazids as a sister group to margaritids (Hickman and McLean, 1990; Hickman, 1996) has not been tested by molecular sequence data. A recent review of *Gaza* and *Callogaza* and description of a ninth species from Brazil (Simone and Cunha, 2006) did not address relationships, but it underscores the global distribution of the group and the potential for undocumented species.

Molecular sequence data for margaritid species resulted in a new phylogenetic hypothesis of the relationship of the family group to other vetigastropods (Williams et al., 2008). However, subsequent analyses have demonstrated that the group is not monophyletic (Williams et. al., 2010). Further molecular genetic analyses are likely to alter the relationship of gazids and margaritids to each other as well as to other vetigastropods (Williams, pers. comm., 2011).

The objectives of this paper are (1) to describe a new gazid genus and two new gazid species, and (2) to provide new data highlighting the unusual features of the group, its biogeography, its ecology, and its role in the deep sea.

The family group ending –idae is used provisionally and without placing Gazidae into a ranked classification of higher taxa of vetigastropods. It does not alter its currently unresolved relationship to the family group Margaritidae, although morphological evidence is presented to suggest that some deep-water species currently assigned to Margaritidae may require re-allocation to Gazidae.

Abbreviations for specimen repositories are: AMS, Australian Museum, Sydney; LACM, Los Angeles County Museum of Natural History, Los Angeles; UCMP, University of California, Berkeley; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.

SYSTEMATICS

Vetigastropoda (unranked)
Family Group Gazidae Hickman and McLean, 1990 (unclassified)

Genus *Callogaza* Dall, 1881

Type Species: By original designation, *Callogaza watsoni* Dall, 1881. Recent, off Havana, Cuba, 24°34′ N, 83°16′ W, 177 fathoms. Distribution: Northern Cuba south to Brazil, 117–500 fathoms.

Description: Shell of 1.5 smooth protoconch whorls and 6 teleoconch whorls with distinct fine spiral and axial sculpture. Smaller than *Gaza* Watson, 1879 (width < 25 mm), relatively broader, and prominently pigmented with alternating white and brown splotches or fine spiral lines on a beige background. Teleoconch whorls shouldered and finely carinate. Umbilical callus thinner than in *Gaza* and convex when completely covering umbilicus.

Callogaza colmani new species

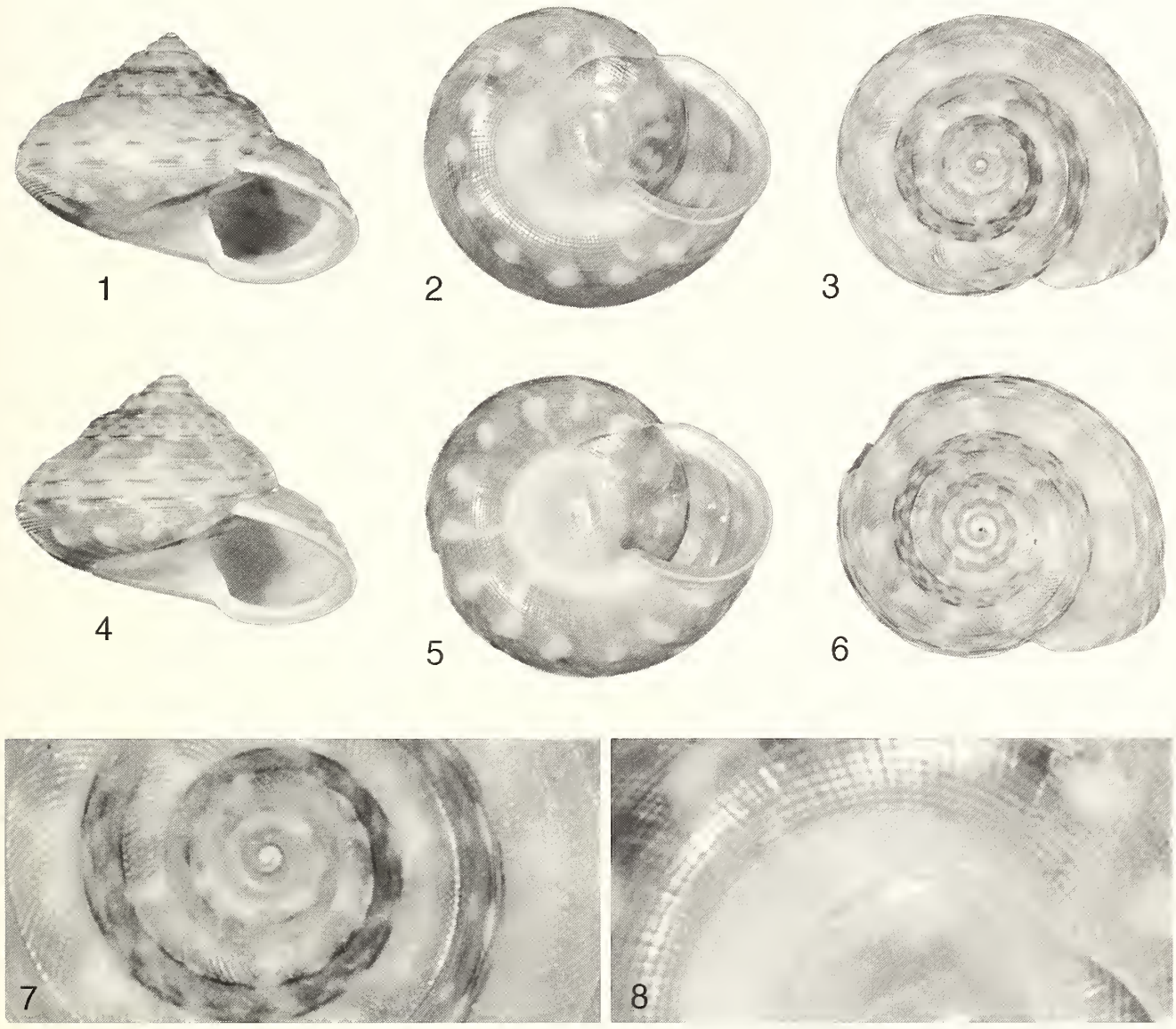
(Figures 1–10, 12, 14–15)

Gaza (*Callogaza*) sp.—Hickman and McLean, 1990, figs. 53b, c, e, f. (originally mislabeled; reported correctly here)

Description (Figures 1–8): Shell width (up to 23.3 mm) exceeds shell height (up to 17.4 mm), and final whorl height exeeeds that of spire. Aperture is strongly prosocline, inclined to axis of coiling at an angle of 50°. Terminal lip both thickened and reflected and marked by a descending suture. Thin, transparent parietal callus continuous from suture to umbilicus, where it is reflexed as a thin, slightly convex covering, creating a closed umbilical chamber. Most abapical of four spiral cords marks periphery of shell, and suture follows fourth spiral. Most apical spiral cord separates a slight shoulder from rest of whorl. On shoulder, 15 very fine spiral lines crossed by slightly stronger, finely spaced axial lines to produce a very finely cancellate surface (Figure 7). A similarly fine cancellate surface occurs between each of pairs of spirals between shoulder and periphery. There are 27 very finely incised spiral lines on base (Figure 8). Shell pigmentation consists of alternating tan and white patches on spiral ribs, with two spiral rows of prominent white blotches on base. Nacre visible only through small windows of transparent shell material and only when shell is moved, generating lustrous flashes. Protoconch is small, glossy, and of 1.5 whorls.

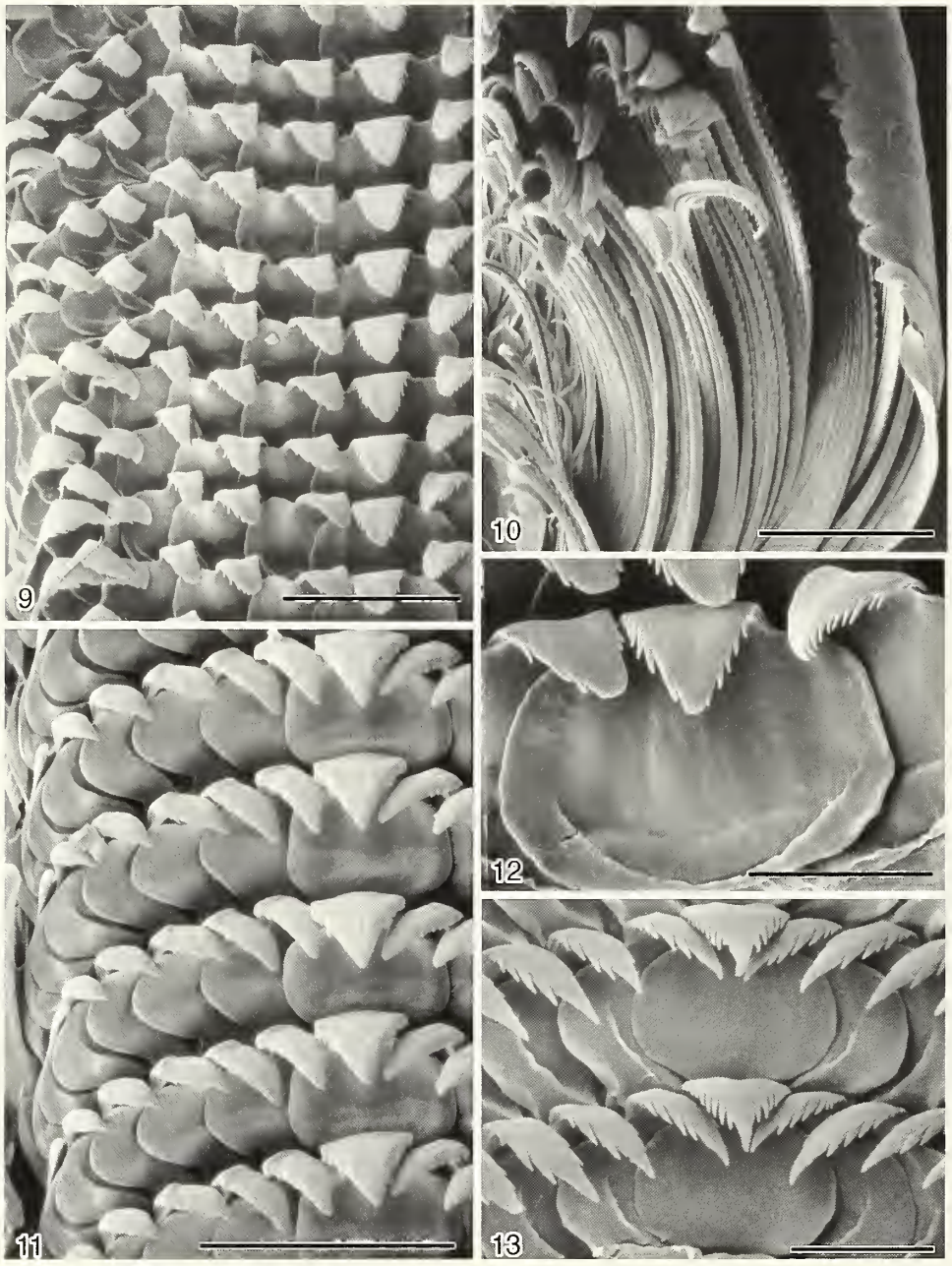
Radula (Figures 9–10, 12): Rachidian is largest tooth in central field. Rachidian tooth with broad, ovate base with triangular over-hanging cusp that emerges directly from base and is finely denticulate along both margins (Figures 9, 12). Seven pairs of lateral teeth present, also with broad bases and triangular, denticulate cusps (Figures 9, 12). Inner portion of each lateral base is obscured by overlapping base of adjacent tooth. Cusp of each lateral tooth directed toward midline, overhanging outer portion of base of adjacent lateral tooth (Figure 9). Outermost lateral teeth with elongate shafts and narrower, longer cusps increasingly curved inward toward rachidian. Between outermost lateral and marginal teeth, in position occupied by lateromarginal plate in generalized troehoidean radula, there are several irregularly-developed tooth bases that have failed to develop shafts and cusps (Hickman and McLean, 1990, Figure 53E, p. 92). Marginal teeth (Figure 10) with extremely long, well-developed shafts and long, narrow, overhanging denticulate cusps. Marginal cusp rows and base rows do not correspond (*sensu* Hickman, 1984a). Prominent serration of the marginal shafts (Figure 10) is a unique feature. Outermost marginal teeth have unusually broad shafts and cusps and may be partially or fully fused to one another (Figure 10).

Exterior Anatomy (Figures 14–15): Deep transverse groove (inferred pedal gland) present along anterior margin of the propodium. In retracted and preserved animal, anterior propodium and mesopodium folded under and against sole of foot, with oral disk of snout



Figures 1–8. *Callogaza colmani* new species. **1.** Apertural, **2.** Basal, and **3.** Apical views of the holotype, AMS 115689, height = 17.4 mm. **4.** Apertural, **5.** Basal, and **6.** Apical views of paratype 1, AMS 115689a, height = 17.9 mm. **7.** Details of sculpture on apical whorls of holotype. **8.** Details of sculpture on base of holotype.

pressed against fold. Large snout cylindrical, expanding distally to a tentacular margin surrounding broad oral dise densely eovered with shorter tentacles. Mouth lies within longitudinal groove on oral disc. Large, black-pigmented eyes lie at distal ends of short, thiek, dorsoventrally flattened eyestalks. Inner basal margins of eyestalks continue over bases of cephalie tentacles, joining small crescent-shaped cephalie lappets. Lappets have entire margins and do not reach midline of snout. Cephalic tentacles relatively long even in their contracted state. No evidence of micropapillae on either cephalie or epipodial tentacles, but this may be a preservation artifact. Left (inhalant) and right (exhalant) neck lobes large and well-developed flaps of tissue with simple margins. Beneath each neeklobe and eontinuing posteriorly along side of foot is a row of prominent upraised papillae, six on right side and seven on left. (It is not known whether these papillae are innervated and sensory in function or glandular and seeretory, although they are referred to here as epipodial sense organs. They are similar in appearance to the epipodial sense organs that are paired posteriorly with each of the epipodial tentacles.) Seven epipodial tentacles present on right side of animal and six on left. Eaeh tentacle and its basal sense organ arise beneath a separate, thin, crescent-shaped flap of epipodial tissue. Epipodial flaps partially overlap one another in imbrieate fashion. Epipodial tentaele length decreases posteriorly on both sides. On left side, anteriormost epipodial tentacle lacks a flap and basal sense organ and is longer and set apart from other five tentacles. Mantle eavity of holotype not dissected, but long free tip

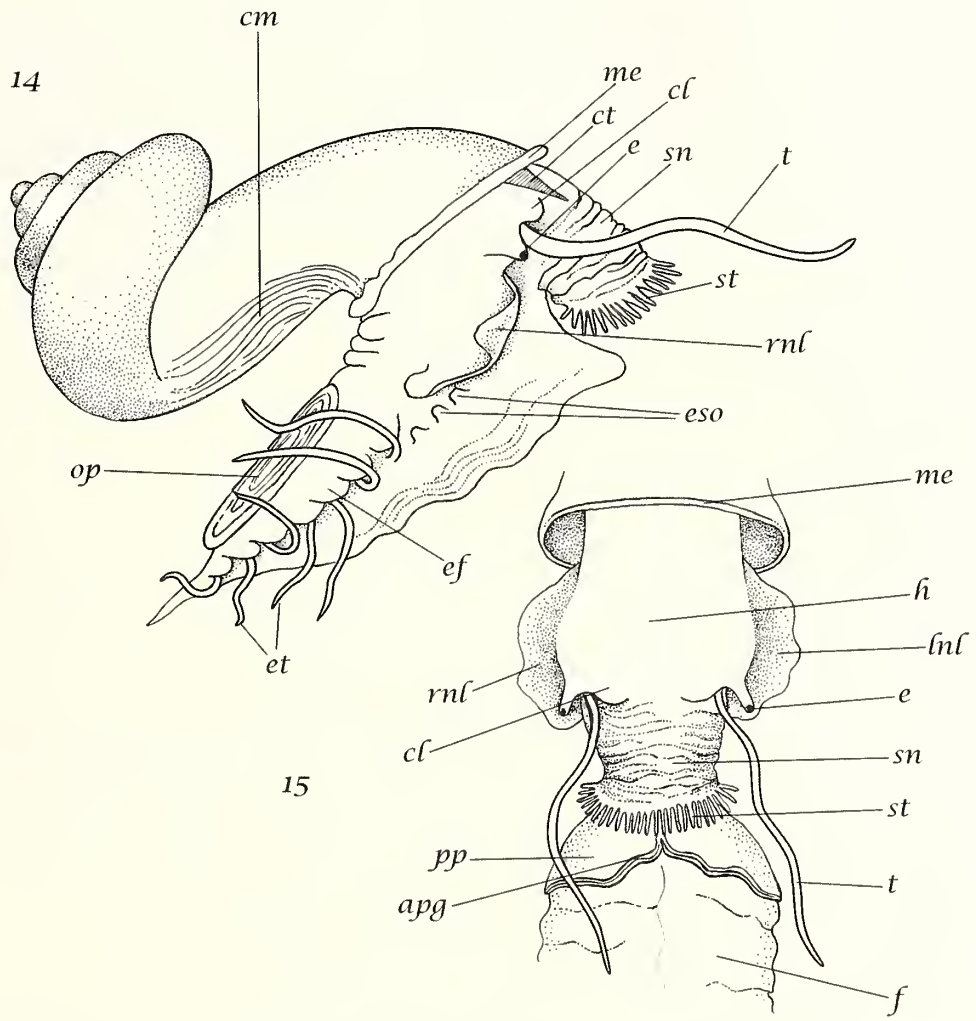


Figures 9–13. Radulae. **9–10, 12.** *Callogaza colmani* new species. **9.** Rachidian and left lateral teeth of holotype, AMS 115689, scale bar = 100 µm. **10.** Right marginal teeth of holotype, bar = 100 µm. **12.** Detail of rachidian base and serration of rachidian and inner lateral cusps of holotype, scale bar = 40 µm. **11.** Rachidian and left lateral teeth of *Gaza superba* Dall, 1881, UCMP D-3763. **13.** Rachidian and inner lateral teeth of *Margarites simbla* Dall, 1913, LACM 71-374.

of bipectinate ctenidium projects from beneath mantle margin of preserved specimen.

Remarks: The new species is distinguished from *Callogaza watsoni*, by complete nacreous terminal closure of the umbilicus and relatively higher spire. The spire is relatively lower than that of *Callogaza sericata* (Kira, 1959) from Japan, which also has a smaller shell, forming its terminal aperture at half the size of adult *C. colmani*. The Japanese species also differs in details of spiral and axial sculpture and pigmentation pattern. Although the pigments are similar, they are distributed differently, as in the arrangement of white splotches on the base of the shell. The radula and soft anatomy are unknown for both *C. watsoni* and *C. sericata*, but the shells have been adequately figured by previous authors (see Simone and Cunha, 2006, Figures 41–48).

The shell has a relatively higher spire than the type species and a relatively lower spire than *Callogaza sericata* (Kira, 1959) from Japan. Although the Japanese species is



Figures 14–15. External anatomy of *Callogaza colmani* new species, holotype (AMS 115689) and paratype 3 (AMS 115689b). **14.** Right lateral view, **15.** Oblique view of head/foot. Abbreviations: **apg**, anterior pedal gland; **cl,** cephalic lappet; **cm,** columellar muscle; **ct,** ctenidium; **e,** eye and eyestalk; **ef,** epipodial flap; **eso,** epipodial sense organ; **et,** epipodial tentacle; **f,** foot (sole of mesopodium); **h,** head; **lnl,** left (inhalant) neck lobe; **op,** operculum; **me**, mantle edge; **p,** propodium; **rnl,** right (exhalant) neck lobe; **sn,** snout; **st,** snout tentacles; **t,** cephalic tentacle.

more similar in the pigments present in the shell, they are patterned differently, as in the arrangement of white splotches on the base of *C. sericata*. The Japanese species has a smaller shell, forming a terminal aperture at half the size of adult *C. colmani*.

This is the first account of the soft parts of *Callogaza*, and the major features link it clearly with *Gaza*. The large number of epipodial tentacles is a feature shared with some species of *Margarites* Gray, 1847, and was a significant factor in classifying Margaritini and Gazini as sister tribes by Hickman and McLean (1990). Isolated epipodial sense organs anterior to the epipodial tentacles do occur in some species of *Margarites*, although isolated papillae also occur beneath the neck lobes in a number of cantharidine gastropods (Hickman personal observation). Series of "holes" or anterior "foot orifices" illustrated in several species of *Gaza* (Simone and Cunha, 2006) are identical in placement on the foot, but there is no evidence of holes or openings in the upraised, papillae on the foot of *Callogaza colmani*.

There is no information on the radula of other species of *Callogaza*. The radula of *C. colmani* is similar to that of *Gaza superba* (Dall, 1881) (Figure 11), although the tooth bases in the central field are thinner and the cusps are thinner and more denticulate. The large number of lateral teeth (>5 per half row) was a shared feature originally linking Gazini and Margaritini (Hickman and McLean, 1990; Hickman, 1996).

The rachidian and lateral teeth of a thin-shelled deep-water species originally described as *Margarites simbla* Dall, 1913 have many features in common with the new species of *Callogaza* and are illustrated here (Figure 13) to call attention to two eastern Pacific species that cannot be allocated at this time. The other species, *Margarites huloti* Vilvens and Sellanes, 2006, was described as part of a Chilean methane seep biota. Both species are

thin-shelled but lack gazid determinate growth features. Vilvens and Sellanes (2006) and Warén et al. (2011) compared *M. luuloti* to two species described from methane seeps off Japan: *Margarites ryukyuensis* Okutani, Sasaki, and Tsuchida, 2000 and *Margarites shinkai* Okutani, Tsuchida, and Fukikura, 1992. However, both of the Japanese species have radulae with margaritid features that include the shapes of the rachidian and lateral teeth, the presence of a lateromarginal plate, and marginal teeth with base rows and cusp rows that correspond with the base and cusp rows of the central tooth complex.

Type Material: Holotype: Australian Museum, Sydney 115689 (shell and figured animal). Figured paratype 1: AMS 115689a (shell and radula). Figured paratype 2: AMS 115689b (animal). Additional paratypes: AMS 115689c–f (shells with preserved animals), Fisheries R/V Kapala Stn. K78-23-09, 6 November 1978.

Dimensions: Holotype: height 17.4 mm, maximum width 23.3 mm. Figured paratype: height 17.9 mm, maximum width 22.9 mm.

Type Locality: Off Point Danger, New South Wales, Australia, 27°55–57′ S, 154°03′ E, 550 m. Point Danger is not recognized as a place name by the Australian Department of Natural Resources, Division of National Mapping. It is, however, on Admiralty Charts used by the Kapala, and P. H. Colman (pers. comm., 2008) traces its origin to 1770 when Captain James Cook gave the name of "Mount Warning" to a prominent feature onshore and "Point Danger" to the corresponding offshore point where shoals lay. Cook further noted: "Point Danger is the boundary point on the coast between NSW and Qld."

Distribution: The bathymetric and geographic distributions of this species are yet to be determined, but the recovery of 7 live specimens in a single dredge haul suggests that it may be locally abundant. The same haul contained three live specimens of another large-shelled vetigastropod, the calliotropid *Calliotropis glypta* (Watson, 1879).

Etymology: Named in honor of Philip H. Colman, formerly of the Australian Museum, Sydney, who was on the dredging expedition and called the material to the attention of the author.

Genus *Anomphalogaza* new genus

Type Species: *Anomphalogaza moluccensis* new species, by monotypy.

Description: Shell lacking umbilicus, shell height (up to 29.2 mm) exceeding shell width (up to 22.1 mm). Interior nacreous layer thickest, covered by two distinct, unpigmented outer layers, No evidence of opalescent sheen from underlying nacreous layer. Nacreous layer, as well as outer layers, thickened and reflexed at terminal aperture. Terminal aperture descending. Nacreous parietal callus divided into two portions, one on upper parietal wall immediately below upper termination of outer lip and other on lowermost parietal wall and connected to columellar callus. Thin, transparent shell layer of unidentified composition superimposed as secondary callus on underlying columellar and parietal callus and continuous across parietal wall. Final whorl sculpture consisting of 130 closely-spaced, very finely-incised spiral lines crossed by fine closely-spaced collabral growth lines, visible only with magnification. Suture slightly adpressed to preceding whorl throughout coiling.

Remarks: The thickened and reflexed outer lip is a unique shared feature of all species of Gazidae. It is accompanied by a descending suture immediately prior to formation of the terminal lip. Both features are indicative of determinate growth. The thin parietal and columellar callus may also be terminal features, but younger individuals will be required to determine if this is the case.

The genus is distinguished from *Gaza* and *Callogaza* by the absence of an umbilicus by and relatively greater shell height. Height exceeds width, and the generating curve is tangent to the axis of coiling, precluding the presence of umbilical space. It is further distinguished from *Callogaza* by larger adult size (>20 mm), lack of pigmentation, and the absence both of axial sculpture and any strong spiral elements or peripheral demarcation. Shells lack the lustrous sheen typical of both *Gaza* and *Callogaza*. The suture is slightly adpressed to the preceding whorl in contrast to the impressed suture in species of *Gaza*, and the aperture is less prosocline.

The shell apex is worn on both holotype and paratype, obscuring the details of protoconch size and early teleoconch sculpture.

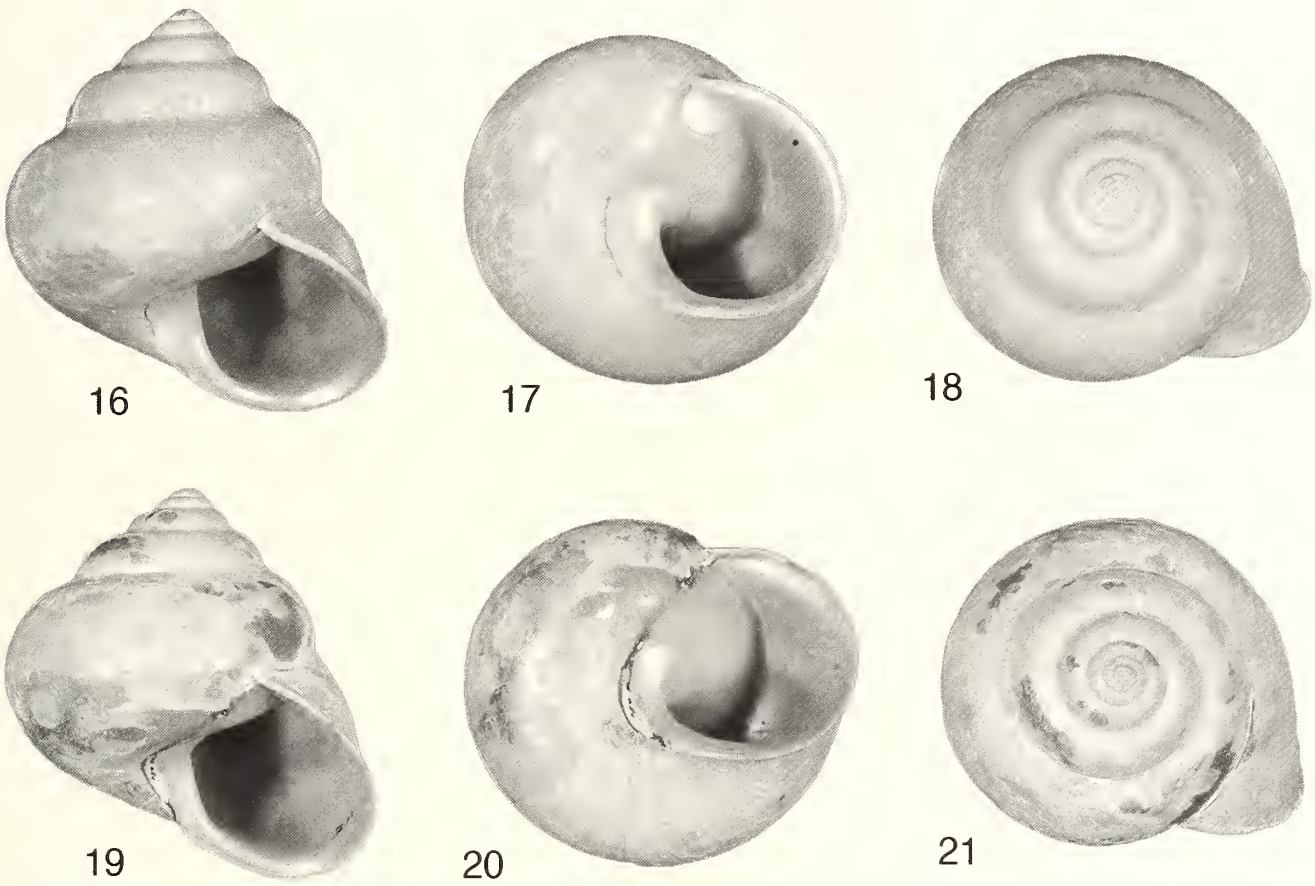
Etymology: *an* (Gr. without) + *omphalos* (Gr. umbilicus), recognizing that there is neither an open umbilicus or an umbilicus that has been sealed over by secretion of a terminal callus deposit.

***Anomphalogaza moluccensis* new species**
(Figures 16–21)

Description: Same as for genus (monotypic genus).

Remarks: The holotype and paratype were both collected as empty shells. Unlike many gazid species, the apex of the shells is not perforated and the shells are free of epi- and endobionts. However, the shell of the paratype is corroded; and the exfoliation of outer shell has exposed the evidence of two distinct layers. Both shells sustained and repaired episodes of sublethal damage to the growing margin of the aperture. On the holotype there are six repaired breakages on the body whorl and eight on the exposed portion of spire whorls. Both specimens repaired an irregular breakage along the entire apertural margin immediately prior to secretion of the terminal apertural rim.

Type Material: Holotype USNM 311367. Paratype USNM 311367b. Both empty shells.



Figures 16–21. *Anomphalogaza moluccensis* new species. **16.** Apertural, **17.** Basal, and **18.** Apical views of the holotype, USNM 311367, height = 29.2 mm. **19.** Apertural, **20.** Basal, and **21.** Apical views of paratype, USNM 311367a, height = 28.0 mm.

Dimensions: Holotype: Height 29.2 mm, maximum width 22.1 mm. Paratype: Height 28.0 mm, maximum width 21.9 mm.

Type Locality: U.S. Fish Commission, R/V Albatross, Station 5601. 13 November 1909. 01°13′10″ N, 125°17′05″ E. Molucca Sea, Indonesia, Celebes (Sulawesi). 765 Fathoms (=1,399 m). Sand, *Globigerina* and pteropods.

Distribution: The genus and species are thus far known from only a single loeality at greater depth than any of the gazid taxa deseribed to date and in a setting that is more geologically remote and isolated. It is isolated by its tectonie setting at the western edge the Molueea Sea Microplate, the only known site of active eollision between two faeing Island Arcs. The geologic eomplexity of this region is treated further in the diseussion beeause it is pertinent to understanding the geologic and evolutionary history of the deep-sea fauna.

DISCUSSION

Biological And Paleobiological Reassessments

Gaza and *Callogaza* have been recognized for many years as conspicuous elements of the tropieal Western Atlantic and Caribbean fauna (Clench and Abbott, 1943). Their relatively large shell sizes and local abundance (Quinn, 1979) have facilitated their use as models for understanding taphonomie and paleoecologieal phenomena in deep-sea gastropods (Walker and Voight, 1994; Voight and Walker, 1995). The *Gaza* Community was designated as an example of a deep-water community type with origins in the Eoeene (Hickman, 1984b). Discoveries of chemosynthetieally nourished eommunities in the northern Gulf of Mexieo (Kennicutt et al., 1985) suggest a potentially unconventional carbon souree for these large gastropods.

Four aspects of the morphology and biology of these gastropods are reeonsidered here: (1) the phenomenon of determinate growth, (2) the high incidence of repair of sublethal shell damage, (3) the umbilicate condition, and (4) the nutritional carbon souree.

Determinate Growth in Gazid Gastropods: Determinate growth is manifest in three morphologieal features of gazid gastropods: (1) reflection and thickening of the outer lip, (2) refleetion of the columellar lip to form a thin eallus eompletely or partially covering the umbilicus, and (3) a deseending suture. It is the only family-group vetigastropod taxon in which all known species develop these three features. The thiekened and reflected lip was

used as a diagnostic feature in proposal of the family-group name (Hickman and McLean, 1990). The thin, translucent, bubble-like callus is, likewise, a unique derived feature of the genus *Callogaza* (Hickman, 1998).

In marine gastropods, determinate growth occurs primarily in siphonate caenogastropods and in shallow-water, tropical habitats (Vermeij and Signor, 1992). It is recognized most often by a terminal elaboration of the aperture, which may be thickened, reflected, or flaired. Other signatures of cessation of spiral growth in caenogastropods include the formation of a distinctive parietal callus that may extend onto the spire and a change in the direction of spiral growth, where it is referred to as an "ascending suture" (Vermeij and Signor, 1992).

Although determinate growth has been considered rare in the basal "archaeogastropod" groups (Vermeij and Signor, 1992), there is increasing evidence of terminal features that do not occur earlier in ontogeny. In contrast to siphonate caenogatropods, changes in direction of spiral growth are typically recorded as a descending suture between the body whorl and penultimate whorl. A descending suture immediately precedes the formation of the thickened terminal lip can be seen in both the new species of *Callogaza* and the new genus *Anomphalogaza*. In other basal gastropod clades a descending suture occurs in some, but not all, species. If there is no terminal modification of the lip, a descending suture may accompany a slowing of growth in the largest individuals. For example, some species of *Clanculus* Montfort, 1810 have a descending suture without any terminal modification of the aperture (Hickman, personal observation). In contrast, a descending suture is paired with a flaired and reflexed aperture in some species of deep-water gastropods in the genus *Calliotropis* Seguenza, 1903 (Hickman, personal observation).

The descending suture forces the spire of the active crawling animal upward, increasing the angle between the axis of coiling and the substrate. Functional significance of the change in coiling geometry is not known, nor is the function of terminal modification of the aperture. Walker and Voight (1994) reported high shell repair frequency in two species of *Gaza* in a study showing that attempted predation is common in large-shelled (>25 mm height) gastropods, although rare in small-shelled species. If the ability to repair apertural damage decreases with age, formation of a thickened terminal aperture may provide an adaptive advantage to reproductively mature adults. Irregular breakages on the shells of *Gaza superba* indicate that there was no terminal thickening at the time the damage occurred.

Shell Repair in Gazid Gastropods: High frequency of shell repair in living and fossil marine gastropods serves as in indicator of predation pressure and of predator ability to survive attempted predation (Vermeij, 1982). Studies of shell repair frequencies on small-shelled gastropods concluded that predation pressure was low in the deep sea (Vale and Rex, 1988, 1989). It is therefore surprising that later studies of large-shelled deep-sea gastropods not only show high repair frequencies but also that the shells of these species lack the typical anti-predator adaptations (Walker and Voight, 1994; Harasewych, 2002). A study of repaired breakage in pleurotomariid gastropods reported "extraordinarily high level of unsuccessful predation for all species examined" (Harasewych, 2002). This is surprising because these species have an uncalcified operculum, relatively thin shell, and open umbilicus that should render them mechanically more vulnerable than taxa with robust shells, no umbilicus, and a heavy calcareous operculum. However, living pleurotomariids also appear to be well defended chemically by a hypobranchial gland secretion that is released in response to disturbance and shell damage (Harasewych, 2002). High shell repair frequencies were also reported in a study of species of *Gaza* and large-shelled species of the calliotropid genus *Bathybembix* Crosse, 1893 (Walker and Voight, 1994).

The Umbilicate Condition in Gazid Gastropods: The terms used to describe the umbilicate condition in gastropods are difficult to apply to gazids because closure of an umbilical opening, if it occurs, is a thin reflected nacreous layer secreted at the cessation of growth. The shell is phaneromphalus until growth ceases and never becomes partially or completely plugged in the sense of hemiomphalous or cryptomphalous. The terminal partial or complete sealing off of the umbilicus partially or completely hides its presence as an empty chamber.

In the new genus *Anomphalogaza*, there simply is no umbilicus, and the terminal columellar and parietal calluses are reflected over shell only: there is no opening to seal off.

The lack of an umbilical plug contributes to the lightness of the shell and low investment in calcium carbonate. The perforation of the apex in some species, rendering the umbilicus open at both ends, is permitted by the lack of filling. The lack of umbilical filling has permitted use of the umbilicus of *Gaza superba* and *Gaza olivacea* Quinn, 1981 by a polychaete that is alleged to create the apical perforation (Quinn, 1991; Voight and Walker, 1995).

Nutritional Carbon Source of Gazid Gastropods: *Gaza* and *Callogaza* have not been identified conclusively as elements of chemosynthetically nourished communities. However, *Gaza superba* and *Gaza fischeri* Dall, 1889 are locally abundant on the upper slope in the Gulf of Mexico in regions of confirmed methane and sulfide seepage (Kennicutt et al., 1985; Carney, 1994). Five new records of *Gaza fischeri* from the Louisiana slope are included in an account of seep and vent gastropods (Warén and Bouchet, 1993). There is no evidence of an enriched photosynthetically derived (detrital) carbon source to support communities dominated by gazid species. However, the alternative possibility of diffuse seepage (*sensu* Nesbitt and Campbell, 2004) supporting chemoautotrophic bacterial synthesis of organic carbon in and on the sediments is worth investigating. Possible sources of enriched dietary carbon also include bacterial degradation of hydrocarbons in sediments (Brooks et al.,

1987). In this instance, the concept of a seep community is not synonymous with chemosymbiosis. It is, however, indicative of an unconventional carbon source.

The enlarged hindguts of these gastropods are packed with sediment, and sedimentary grain coatings have been implicated as a significant source of nutrition for large deposit-feeding gastropods that selectively ingest grains with the greatest surface area to volume ratio (Hickman, 1981). The earliest occurrences (late Eocene) of large-shelled calliotropid gastropods of the genus *Bathybembix* are in a geological setting of both discrete and diffuse methane seepage on an active continental margin (Hickman, 2003).

Biogeographic Reassessment

The new taxa described here call attention to a more global biogeographic pattern and to extra-tropical occurrences in the Western Pacific. *Callogaza colmani* is the first representative of the family recognized from the Australian plate with its Gondwanan origin and history. *Anomphalogaza moluccensis* is the first gazid described from the biogeographic region of Wallacea. Indonesia as political and modern geographic unit has been assembled over the past 55 million years from complex tectonic evolution of major plate boundaries and microplates. In the Eocene, present day Sulawesi (although not emergent as land) was situated south of Borneo and west of its present location in eastern Indonesia (Hall, 2001). The type locality for the new gazid genus and species is on the disappearing western boundary of what was once a large sea. The ancient Molucca Sea has been squeezed and subducted by convergence of the Philippine Sea Plate, the Australian Plate, and the Eurasian Plate (Widiwijayanti et al., 2003). The disappearance of the Molucca Sea has received considerable attention because it is the only present-day example of active collision between two facing volcanic arc-trench systems. Subduction beneath Halmahera to the east and beneath Sulawesi to the west is consuming the last of the microplate (McCaffery et al., 1980; Hall et al., 1995; Hall, 2000). The thick, deformed seafloor collision complex trapped between north arm of Sulawesi and Halmahera is, at minimum, only 250 km in width (McCaffrey et al., 1980). The potential marine biogeographic importance of this complex history is that the shrinking ocean basin in which *Anomphalogaza* occurs will have disappeared in another three million years (Hickman, 2009).

The northern Arm of Sulawesi, the Molucca Sea, and Halmahera are situated at the northern edge of the biogeographic region of Wallacea in the region of least distance between Wallace's Line and Lydekker's Line. The sharp terrestrial biogeographic breaks that define Wallacea have been considered invisible to shallow marine taxa, although there are recent challenges that suggest a "marine Wallace's line" (Barber et al., 2000). For the deep-water fauna, the concept of Wallacea requires greater attention to structural features, tectonics, and longer geologic history (see Lee and McCabe, 1986). With the knowledge that active plate margins are sites of venting and seepage fueling chemosynthetically based communities, it is now possible to target sites that have never been sampled for chemosymbiotic taxa in the waters of Southeast Asia and the SW Pacific.

FUTURE DIRECTIONS

New morphological and anatomical data from this report, combined with detailed anatomical data from a new Brazilian species (Simone and Cunha, 2006) are consistent with previous morphological inference of gazid monophyly, regardless of rank and classification. The novel combination of features of shell, radula, anatomy, nutrition, and ecology distinguish it from other vetigastropod family groups. However, the relationships of family groups of vetigastropods are still poorly resolved, and morphological data presented here do not address phylogenetic relationships. For the morphologist, the challenge lies in unmasking convergence.

Strong morphological convergence in deep-sea vetigastropods is clearly related to deep-sea benthic ecology and deposit-feeding (Hickman, 1981, 1984b, 2003). The enlarged hindgut, expanded and tentacular oral disk margin, and anteriolateral expansion of the foot also occur in large, deposit-feeding seguenzioid gastropods such as species of *Bathybembix* Crosse, 1893 and *Calliotropis* Seguenza, 1903, a genus that is unusually abundant and speciose at bathyal depths throughout the world and especially in the Indo-Pacific (Vilvens, 2007). Shells also have converged on visibility of nacre through an extremely thin outer shell layer and terminal growth features that include flaring or thickening of the terminal aperture, a descending suture, and reflection of the columellar callus to partially or fully cover (but not fill) the umbilicus (Hickman, personal observation).

Thinning of the shell and terminal growth features are also common convergent shell features in several deep-water skeneiform gastropod groups (Hickman, personal observation). In describing the enigmatic Australasian family group Kaiparathini (under Margaritinae), Marshall (1993), noted several anatomical similarities to *Gaza superba*. Kaiparathinids do not fit comfortably into existing vetigastropod classification.

The genus *Margarites* Gray, 1847 needs both morphological and molecular work to identify taxa that belong elsewhere. More than 50 species have been assigned to the genus. In addition to the deep-water species noted above as candidates for transfer to Gazidae, there are extinct deep-water species dating back to the Cretaceous. Kaim et al. (2009) described *Margarites sasakii* from a Campanian cold seep site in northern Hokkaido, Japan, indicating deep origins of vetigastropods in chemosynthetically based communities. Deep-water fossil species are also described from Eocene cold-seep carbonates in Paleogene rocks in the Pacific Northwest (e.g. Squires and Goedert, 1991).

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LITERATURE CITED

Barber, P.H., S.R. Palumbi, M.V. Erdmann, and M.K. Moosa. 2000. A marine Wallace's line? Nature 406: 692–693.

Bouchet, P. and J.-P. Rocroi, (eds.). 2005. Classification and Nomenclator of Gastropod Families. Malacologia 47: 1–397.

Brooks, J.M., M.C. Kennicutt II, C.R. Fisher, S.A. Macko, K. Cole, J.J. Childress, R.R. Bidigare, and R.D. Vetter. 1987. Deep-sea hydrocarbon seep communities: evidence for energy and nutritional carbon sources. Science 238: 1138–1142.

Carney, R.S. 1994. Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents. Geo-Marine Letters 14: 149–159.

Clench, W.J. and R.T. Abbott. 1943. The genera *Gaza* and *Livona* in the Western Atlantic. Johnsonia 12: 1–12.

Geiger, D.L. and C.E. Thacker. 2005. Molecular phylogeny of Vetigastropods reveals non-monophyletic Scissurellidae, Trochoidea, Fissurelloidea. Molluscan Research 25: 47–55.

Hall, R. 2000. Neogene history of collision in the Halmahera region, Indonesia. Proceedings of the Indonesian Petroleum Association, 27th Annual Convention, pp. 487–493.

Hall, R. 2001. Cenozoic reconstructions of Southeast Asia and the SW Pacific: changing patterns of land and sea. In: L. Metcalfe, J.M.B. Smith, M. Morwood and I.D. Davidson (eds.) Faunal and Floral Migrations and Evolution in SE Asia-Australasia. A.A. Baklkema, Lisse, pp. 35–56.

Hall, R., J.R. Ali, C.D. Anderson, and S.J. Baker. 1995. Origin and motion history of the Philippine Sea Plate. Tectonophysics 251: 229–250.

Harasewych, M.G. 2002. Pleurotomarioidean gastropods. Advances in Marine Biology 42: 237–295.

Hickman, C.S. 1981. Selective deposit feeding by the deep-sea archaeogastropod *Bathybembix aeola*. Marine Ecology Progress Series 7: 339–342.

Hickman, C.S. 1984a. Implications of radular tooth-row functional integration for archaeogastropod systematics. The Veliger 26(2): 189–194.

Hickman, C.S. 1984b. Composition, structure, ecology, and evolution of six Cenozoic deep-water mollusk communities. Journal of Paleontology 58: 1215–1234.

Hickman, C.S. 1996. Phylogeny and patterns of evolutionary radiation in trochoidean gastropods. In: J.D. Taylor (ed.) Origin and Evolutionary Radiation of the Mollusca. Oxford University Press, Oxford, pp. 177–198.

Hickman, C.S. 1998. Subfamily Margaritinae. In: P.L. Beesley, G.J.B. Ross and A. Wells (eds.) Mollusca: the Southern Synthesis. Fauna of Australia. V. 5, CSIRO Publishing: Melbourne, Part B, viii, pp. 682–683.

Hickman, C.S. 2003. Evidence for abrupt Eocene-Oligocene molluscan faunal change in the Pacific Northwest. In: D.R. Prothero, E.A. Nesbitt and L. Ivany (eds.) From Greenhouse to Icehouse: The Marine Eocene–Oligocene Transition. Columbia University Press, New York, pp. 71–87.

Hickman, C.S. 2009. Relict deep-water gastropods in a disappearing seaway. Program and Abstracts – American Malacological Society 75th Annual Meeting. Paleontological Research Institution Special Publication 37: 45.

Hickman, C.S. and J.H. McLean. 1990. Systematic revision and suprageneric classification of trochacean gastropods. Natural History Museum of Los Angeles County Science Series 35: 1–69.

Kaim, A., R.G. Jenkins, and Y. Hikida. 2009. Gastropods from Late Cretaceous Omagari and Yasukawa hydrocarbon seep deposits in the Nakagawa area, Hokkaido, Japan. Acta Palaeontologica Polonica 54(3): 463–490.

Kano, Y. 2008. Vetigastropod phylogeny and a new concept of Seguenzioidea: independent evolution of copulatory organs in the deep-sea habitats. Zoologica Scripta 37: 1–21.

Lee, C.S. and R. McCabe. 1986. The Banda–Celebes–Sulu basin: a trapped piece of Cretaceous–Eocene oceanic crust? Nature 332: 51–54.

Kennicutt, M.C., II, J.M. Brooks, R.R. Bidigare, R.R. Fay, T.L. Wade, and T.J. McDonald. 1985. Vent-type taxa in a hydrocarbon seep region on the Louisiana slope. Nature 317: 351–353.

McCaffrey, R., E.A. Silver, and R. Raitt. 1980. Crustal structure of the Molucca Sea collision zone, Indonesia. In: D.E. Hayes (ed.) The Tectonic and Geological Evolution of Southeast Asian Seas and Islands. American Geophysical Union Geophysical Monograph 23: 161–177.

Marshall, B.A. 1993. A review of the genus *Kaiparathina* Laws, 1941 (Mollusca: Gastropoda: Trochoidea). The Veliger 36: 185–198.

Nesbitt, L.A. and K.A. Campbell. 2004. Spatial and stratigraphic distribution of fossils from diffuse seeps in a Pliocene shelf setting, Cascadia convergent margin. Geological Society of America Abstracts with Programs 36(5): 314.

Quinn, J.F., Jr. 1979. Biological results of the University of Miami Deep-sea expeditions. 130. The systematics and zoogeography of the gastropod family Trochidae collected in the Straits of Florida and its approaches. Malacologia 19: 1–62.

Quinn, J.F., Jr. 1991. New species of *Gaza*, *Mirachelus*, *Calliotropis*, and *Echinogurges* (Gastropoda: Trochidae) from the Northwestern Atlantic Ocean. The Nautilus 105: 166–172.

Simone, L.R.L. and C.M. Cunha. 2006. Revision of genera *Gaza* and *Callogaza* (Vetigastropoda, Trochidae) with description of a new Brazilian species. Zootaxa 1381: 1–40.

Squires, R.L. and J.L. Goedert. 1991. New late Eocene mollusks from localized deposits formed by subduction-related

methane seeps, southweswtern Washington. Journal of Paleontology 65: 412–416.

Vale, F.K. and M.A. Rex. 1988. Repaired shell damage in the deepsea prosobranch gastropods from the western north Atlantic. Malacologia 28: 65–79.

Vale, F.K. and M.A. Rex. 1989. Repaired shell damage in a complex of rissoid gastropods from the upper continental shelf south of New England. Nautilus 103: 105–108.

Vermeij, G.J. 1982. Gastropod shell form, breakage and repair in relation to predation by the crab *Calappa*. Malacologia 231: 1–12.

Vermeij, G.J. and P.W. Signor. 1992. The geographic, taxonomic and temporal distribution of determinate growth in marine gastropods. Biological Journal of the Linnean Society 47: 233–247.

Vilvens, C. 2007. New species and new records of *Calliotropis* (Gastropoda: Chilodontidae: Calliotropinae) from Indo-Pacific. Novapex 5: 1–72.

Vilvens, C. and J. Sellanes. 2006. Descriptions of *Otukaia crustulum* new species (Gastropoda: Trochoidea: Calliostomatidae) and *Margarites huloti* new species (Gastropoda: Trochoidea: Trochidae) from a methane seep area off Chile. The Nautilus 120: 15–20.

Voight, J.R. and S.E. Walker. 1995. Geographic variation of shell bionts in the deep-sea snail *Gaza*. Deep Sea Research 42: 1261–1271.

Warén, A. and P. Bouchet. 1993. New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. Zoological Scripta 22: 1–90.

Warén, A., T. Nakano, and J. Sellanes. 2011. A new species of *Iothia* (Gastropoda: Lepetidae) from Chilean methane seeps, with comments on the accompanying gastropod fauna. Nautilus 125: 1–14.

Walker, S.E. and J.R. Voight. 1994. Paleoecologic and taphonomic potential of deep-sea gastropods. Palaios 9: 48–59.

Widiwijayanti, C., V. Mikhailov, M. Diament, C. Deplus, R. Louat, S. Tikhotsky, and A. Gvishiani. 2003. Structure and evolution of the Molucca Sea area: constraints based on interpretation of a combined sea-surface and satellite gravity dataset. Earth and Planetary Science Letters 215: 135–150.

Williams, S.T. and T. Ozawa. 2006. Molecular phylogeny suggests polyphyly of both the turban shells (Family Turbinidae) and the superfamily Trochoidea (Mollusca: Vetigastropoda). Molecular Phylogenetics and Evolution 39: 33–51.

Williams, S.T., S. Karube, and T. Ozawa. 2008. Molecular systematics of Vetigastropoda: Trochidae, Turbinidae and Trochoidea redefined. Zoologica Scripta 37: 483–506.

Williams, S.T., K.M. Donald, H.G. Spencer, and T. Nakano. 2010. Molecular systematics of the marine gastropod families Trochidae and Calliostomatidae (Mollusca: Superfamily Trochoidea). Molecular Phylogenetics and Evolution 54: 783–809.

Yoon, S.K. and W. Kim. 2005. Phylogenetic relationships among six vetigastropod groups (Mollusca, Gastropoda) based on 18S rDNA sequences. Molecules and Cells 19: 283–288.

A taxonomic revision of the genus *Trochita* Schumacher, 1817 (Gastropoda: Calyptraeidae) from the southwestern Atlantic

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ABSTRACT

The authors revised the Atlantic species of the genus *Trochita*. Two valid species are recognized. *Trochita pileus* (Lamarck, 1822) and *T. pileolus* (d'Orbigny, 1841) are redescribed and the type material of each species is illustrated. Both species range from the coast of Buenos Aires province to Tierra del Fuego. *Trochita pileus* is a common subtidal Patagonian species and *T. pileolus* is rare and usually lives in deeper waters. *Trochita trochiformis* a Pacific only species is compare with the Atlantic representatives. Protoconch ornamentation and septum margin are the main differences between both Atlantic species. *Trochita georgiana* Powell is a junior synonym of *T. pileolus*.

Additional keywords: Argentina, Patagonia, geographic distribution

INTRODUCTION

The South American species belonging in the genus *Trochita* Schumacher, 1817 were known since early times in historical malacological literature (e.g. Born, 1778; Gmelin 1791; Lamarck, 1822). Many names were proposed from different regions, perhaps, because of the large range of some of the species and its significant conchological variation. Rehder (1943), in a short paper, provided an initial account of the actual type species of the genus *Trochita* and discussed some of the names in use. Nevertheless, he did not illustrate shells, and some older names were not included.

In this revision, we focused on the southwestern Atlantic species of *Trochita*, however, because of proximity and similarity one Pacific form is also included. Type specimens, protoconchs, and radulae of all species are illustrated and redescribed.

MATERIALS AND METHODS

All the material considered is essentially housed at the Invertebrate collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN-In). Some other specimens were studied at the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM) and Museo de La Plata, (MLP). Type material is deposited at Natural History Museum, London, (NHMUK), Museo Nacional de Historia Natural, Santiago, Chile (MNHNS), and Muséum d'Histoire naturelle de Genéve, Switzerland (MHNG). Material from the USNM was originally collected by the United States Antarctic Program (USAP) and was collected by three ships: R/V Hero, R/V Eltanin and R/V Professor Siedlecki. Several lots were also collected during two oceanographic cruises aboard of the argentine B/I Puerto Deseado.

Radulae were prepared according to the method described in Pastorino (2005) and observed using a Philips XL 30 scanning electron microscope (SEM) at the MACN.

Photographs were taken using a digital camera Nikon D100 with a 60 mm Micro lens. All images were digitally processed.

SYSTEMATICS

Family Calyptraeidae Lamarck, 1809

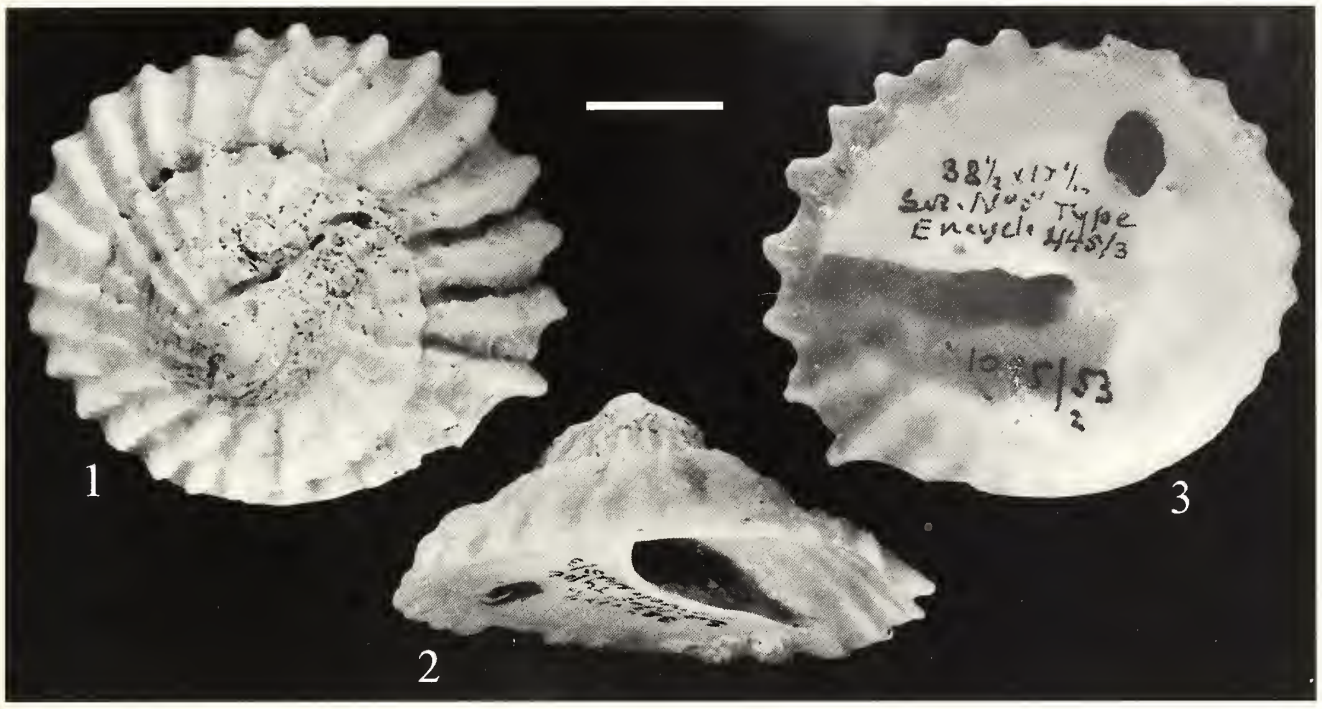
Genus *Trochita* Schumacher, 1817

Type Species: *Trochus spiralis* Schumacher, 1817 (=*Trochus radians* Lamarck, 1816) by SD of Rehder, 1943 (=*Trochita trochiformis* (Born, 1778)).

Trochita trochiformis (Born, 1778)

(Figures 1–3)

Unnamed Knorr, 1768: pl. 29, fig. 1, 2.
Turbo trochiformis Born, 1778: 355.
Patella trochiformis varietas (β) Gmelin, 1791: 3694.
Trochus radians Lamarck, 1816: 445, figs. 3a, b; 1822: 11.
Infundibulum radians.—Sowerby in Gray, 1839: 148, pl. 39, fig. 10.



Figures 1–3. *Trochita trochiformis* (Born, 1778), holotype of *Trochus radians* Lamarck, 1816, MHNG1095/53. Scale bar = 1 cm.

Infundibulum radians. Var.—Sowerby in Gray, 1839: 148, pl. 39, fig. 11.
Trochita radians Lamarck.—Rehder, 1943: 42–43, fig. 1.
?*Trochita spirata* Forbes, 1852: 271, pl. 11, figs. 1a,b.
?*Trochita spirata* Forbes, 1850.—Reeve, 1859: pl. 2 fig. 8.
Calyptraea (*Trochita*) *trochiformis* (Born, 1778).—Keen, 1971: 456, fig. 804; Marincovich, 1973: 31–32, fig. 65; Cañete & Ambler, 1992 (development).
Trochita trochiformis (Born, 1778).—Reid & Osorio, 2000: 124, figs. 3H,I.
Trochita calyptraeformis (Born, 1778).—Collin, 2003a: 550, fig. 2I, 9C; Collin, 2003b: in table 1 and 2; Collin, 2003c: 618–640; Paredes & Cardoso, 2007: 182, fig. 2g; Cañete et al., 2007: 1–7.

Type Material: [*Turbo trochiformis*] not found; [*Trochus radians*] is housed at MHNG1095/53.

Type Locality: [*Turbo trochiformis*] unknown; [*Trochus radians*] "*mer des Antilles, proche la Guadeloupe*".

Other Material Examined: Chile: La Cuchara beach, South of Tocopilla, 4 sp., MLP12091; Coquimbo, 8 sp., MACN-In24810; Antofagasta, 4 sp., MACN-In19580; Antofagasta, 5 sp., MACN-In15090; Antofagasta, several sp. MACN-In24745; Valparaiso, 1 sp, MACN-In29685; Valparaiso, 4 sp., MACN-In25374; Caldera, 3 sp., MACN-In9478;Caldera, 1 sp., MACN-In7321; Caldera, 1 sp. MACN-In 11597-1; Bahía Tangoi, 4 sp., MACN-In24795; Caleta Horcón, 2 sp., MACN-In26030; Talcahuano, 1 sp., MACN-In13815; Puerto San Antonio, Provincia de Santiago, 6 sp., MACN-In12866; Costas de Chile, 4 sp., MACN-In12164.

Distribution: According to Rehder (1943) after material housed at the USNM, from Manta, Ecuador (1° S) to Valparaiso (33° S), Chile. Later Keen (1971), Taylor and Smythe (1985), and, Cañete and Ambler (1992) copy this distribution. Reid and Osorio (2000) collected material of this species in Estero Elefantes, Chile (~45° S). This is the southernmost locality. Paredes and Cardoso (2007) cited the whole peruvian littoral and put some doubt on northern citations.

Vokes (1975) cited Nicklès (1950) as the source of the presence of *T. trochiformis* in Cape Verde Is. and Angola, Africa. Rehder (1943) reported *Trochita* sp. after one worn specimen that could be identified also as *T. trochiformis*. Finally, Taylor and Smythe (1985) mentioned "specimens very similar and probably conspecific with *T. trochiformis*" from the same African region in the collection of the NHMUK. Vokes (1975) discussed the possibility that the same species could be distributed in these two really far away regions travelling by ocean currents. There is no modern study that assures this hypothesis. So far, there is no record of this species, adults or juveniles, in the Argentine littoral. It is difficult to accept that a non-free larvae species travels all the way through the whole Atlantic Ocean. However, despite the direct development of *T. trochiformis* (see Cañete & Ambler, 1992), according to Cañete et al. (2007) this species performs a very particular way of moving during the juvenile stage through planktonic drifting. Nevertheless,

the African distribution of this Pacific only species should be at least treated with care.

Remarks: *Trochita trochiformis* is probably one of the commonest species of *Trochita* from the Pacific coast of South America. It is commercially exploited in Chile and Peru, however, the exact distribution range is somewhat imprecise because of many names locally still in use by local authors. Collin (2003a, b), Cañete et al. (2007) and, Paredes and Cardoso (2007) changed the name to *T. calyptraeformis* (Born, 1778) without any explanation. Born (1778) never proposed this name. Perhaps the confusion started with the species *Sigapatella calyptraeformis* (Lamarck, 1822) a valid species sometimes known under the genus *Calyptraea* from Australia.

One of the main differences with the Atlantic species is the size of the shell which is larger than both, *T. pilens* and *T. pileolus*. Nevertheless, younger, small specimens of *T. troehiformis* could be confused with *T. pilens*, however the number and appearance of ribs clearly differentiate both species. *T. troehiformis* always has coarse ribs, thick shells and more than 25 ribs per whorl. *T. pileus* when present has thin, closely arranged ribs which continue through the suture of the next whorl. In addition the septum of *T. pileus* is clearly sigmoid, with a characteristic initial (central) portion of septum reflexed. *T. trochiformis* usually has an almost straight septum margin. Futhermore, the umbilicus is visible in *T. pileus* and partially hidden in *T. trochiformis*.

***Trochita pileolus* (d'Orbigny, 1841)**
(Figures 4–12, 22–24, 34–39, 40)

Calyptraea (Troehatella) pileolus d'Orbigny, 1841: 463.
Infundibulum pileolus d'Orbigny, 1847: pl. 78, figs. 5, 6, 6'.
Calyptraea deeipiens Philippi, 1845: 61.
Calyptraea Sigapatella pileolus d'Orb.—Tryon, 1886: 122, pl. 35, figs. 91,100.
Calyptraea pileolus d'Orbigny, 1841.—Carcelles, 1950: 57.
Calyptraea (Troehita) georgiana Powell, 1951: 127, Fig. E 3, pl. 7, fig. 22; Zelaya, 2005: 119, fig. 24.

Description: Shell conical, white, short, of 3 convex whorls, of less than 2 cm of maximum diameter and less than 1 cm of maximum height (H/W=0.53 ±0.07, n=36); apex central; protoconch of about 1.5 whorls, slightly excavated; first whorl of protoconch smooth, then 5–6 spiral ribs that vanish towards the teleoconch; teleoconch with irregular concentric growth wrinkles; aperture circular; umbilicus conspicuous, visible, always present; septum straight, slightly sigmoid to the edge; periostracum usually present, pale yellowish, transparent to dark brown.

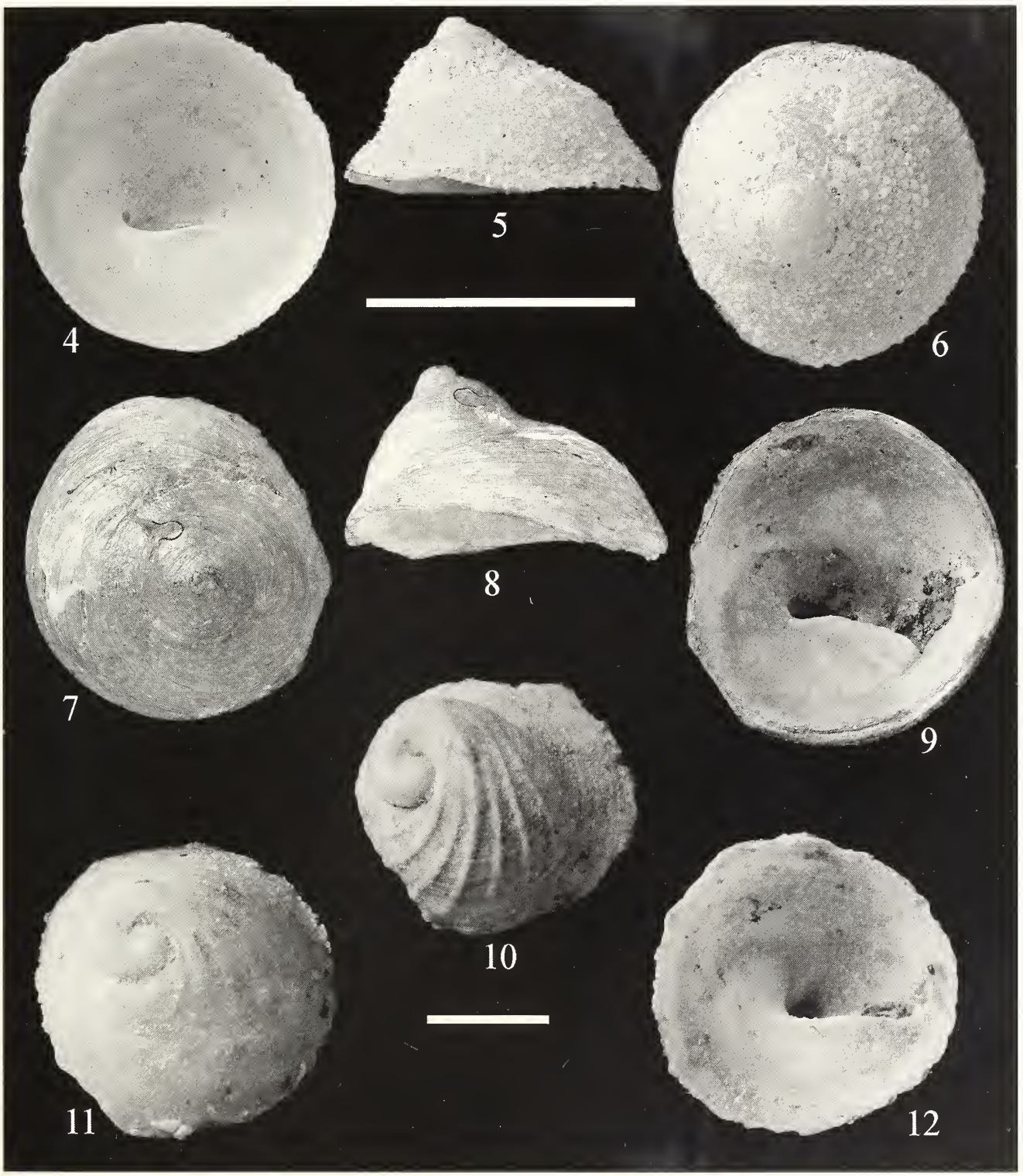
Radula taenioglossate, rachidian tooth rectangular with one central cusp and 3–4 small (obsolete) denticles on each side; lateral tooth broad, with apical cusp toward rachidian line and 7–8 irregular denticles on the external side; two marginal teeth long, curved tall tip sharply pointed without any trace of denticles.

Type Material: [*Calyptraea (Trochatella) pileolus*] 6 syntypes, NHMUK1854.12.4.567; [*Calyptraea (Troehita) georgiana*] holotype, NHMUK 1961469; [*Calyptraea deeipiens*] not seen, probably in Museum für Naturkunde, Berlin (according to Ihering, 1907: 150).

Type Locality: [*Calyptraea (Troehatella) pileolns*] "*Iles Malonines et le eontinent amerieain, sur la cote de la Patagonie meridionale*"; [*Calyptraea decipiens*] "*fretum Magellanicnm*"; [*Calyptraea (Troehita) georgiana*] near Shag Rocks, west of South Georgia, 53°43′40″S, 40°57′ W in 177 m.

Other Material Examined: Argentina: 38°46′53″ S, 55°50′30″ W, in 97 m, St. 7 B/I Puerto Deseado, 1 sp., MACN-In39304; 38°50′56″ S, 55°39′08″ W, in 114 m, St. 8 B/I Puerto Deseado, 4 sp. MACN-In39303; 39°00′ S, 57° 10′ W, 1 sp. in 177–182 m, MACN-In15225; Ría Santa Cruz, 6 sp., MACN-In5171-1; 39°52′37.9″ S, 59°38.6′ W, St. 22, B/I Puerto Deseado, in 96 m, 1 sp., MACN-In39305; 54°28′58.5″ S, 64°57′24.6″ W, St. 1, B/I Puerto Deseado, in 106 m, 4 shells, MACN-In39306; 54°54′ S, 66°19′ W, 8 sp. in about 27 m, MACN-In24017; Punta Sinaia, Tierra del Fuego, 7 sp., MACN-In12541; 51°46′ S, 68°45′ W, 23 sp. in 22 m, MACN-In23858; 54°47′ S, 63°35′ W, 2 sp. in 146 m, MACN-In22293; 54°50′ S, 64°01′ W, 3 sp. in 154 m, MACN-In22734-1; 55°41′ S, 66°34′ W, 1 sp. in 115m, MACN-In24980-1; Bahía Buen Suceso, Tierra del Fuego, 3 sp., MACN-In25072-1; Ushuaia, Tierra del Fuego, 2 sp., MLP13485; Tierra del Fuego, 1 sp., MACN-In20496-1; Puerto Parry, Isla de los Estados, 5 sp., MACN-In21918; Puerto San Juan, Isla de los Estados, 1 sp., MACN-In22160-1; Punta Colnett, Isla de los Estados, 1 sp., MACN-In22566-1; Puerto Olla, Isla Observatorio, 1 sp. in 18–36 m, MACN-In22037-1; Bahía Cumberland, South Georgia Is., 1 sp. in 22 m, MACN-In13537; Bahía Cumberland, 1 sp. in 36 m, MACN-In18969; Schlieper Bay, South Georgia Is., 1 sp., in 18 m, MACN-In18972; Annenkov Is., South Georgia, 3 sp. in 36 m, MACN-In18971; Larsen Harbour, South Georgia Is., 3 sp. in 27 m, MACN-In18970; 53°32′ S, 41°37′ W, Shag Rocks, 1 sp., MLP7252; 54°30′ S, 35°50′ W, 1 sp. in 94 m, MLP7284; Antarctic Bay, South Georgia Is., 2 sp. in 36 m, MACN-In18973; 53°58′ S, 37°09′ W, 1 sp. in 138 m, MACN-In36293; 53°08′ S, 35°25′ W, 1 sp. in 115 m, MACN-In36292. Chile: Isla Nueva, 2 sp., MACN-In24957-1; Puerto Harris, Isla Dawson, 3 sp., MACN-In12432-1; Punta Arenas, 2 sp. MACN-In12390; Punta Arenas, 5 sp., MACN-In13118; Puerto Harris, Isla Dawson, 1 sp., MACN-In14000-1; Puerto Harris, Isla Dawson, 6 sp., MACN-In12482-1.

Distribution: Off Buenos Aires province, in about 100 m depth; subtidal from southern Santa Cruz province (~50°S), Tierra del Fuego, Isla de los Estados, Malvinas (Falkland) Is., South Georgia Is. in Argentina, to Punta Arenas and Isla Dawson in Chile.



Figures 4–12. *Trochita pileolus* (d'Orbigny, 1841). **4–6.** Holotype of *Calyptraea (Trochita) georgiana* Powell, 1951 NHMUK1961469. **7–12.** Three (7–9, 10, 11–12) syntypes of *Calyptraea (Trochatella) pileolus* d'Orbigny, 1841 NHMUK1854.12.4.567. Scale bars: 4–9 = 1 cm, 10–12 = 1 mm.

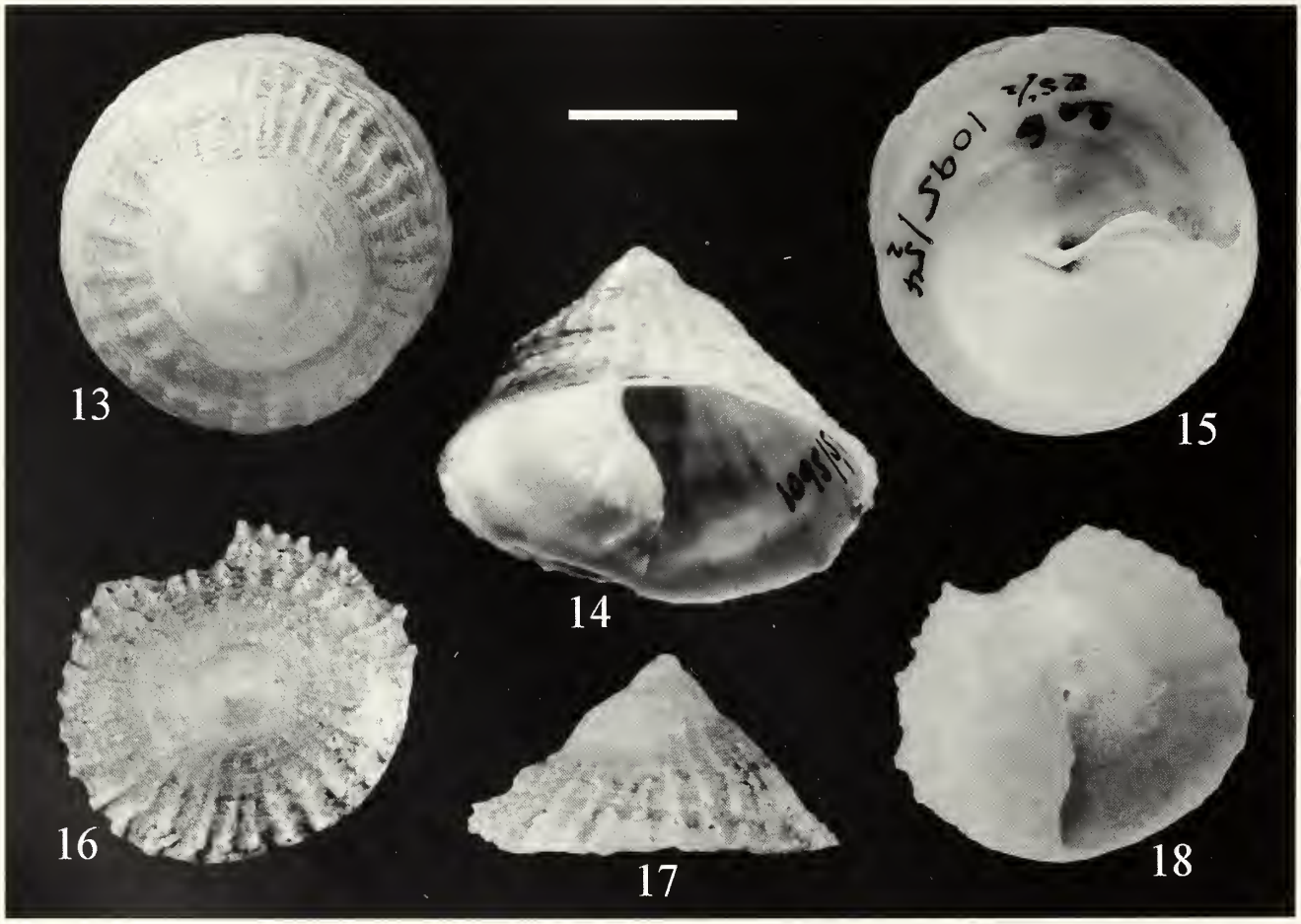
Remarks: This is a typical example of a magellanic species distributed along the whole malacological province. It is subtidal in the southern region and becomes a deep water (~100 m) species on the northern part of its distribution. It was found usually mixed with specimens of *Trochita pileus* both on museum lots and on several unsorted samples. However, it is easily distinguished by the spirals on the protoconch, the open umbilicus and the straight septum. In addition, it is smaller than *T. pileus* and never presents ribs. Most of the specimens, including the holotype of *T. georgiana*, are covered, sometimes by up to three different species of bryozoans and/or sponges. Despite that both species, *T. pileolus* and *T. pileus*, appear together in the samples the latter is the only one that regardless the smooth surface participates of this association.

Ihering (1907) mentioned *T. decipiens* as a synonym of *T. pileolus* and according to him he has seen the type material of Philippi's species. The size and short description of *T. decipiens* agree with this author idea.

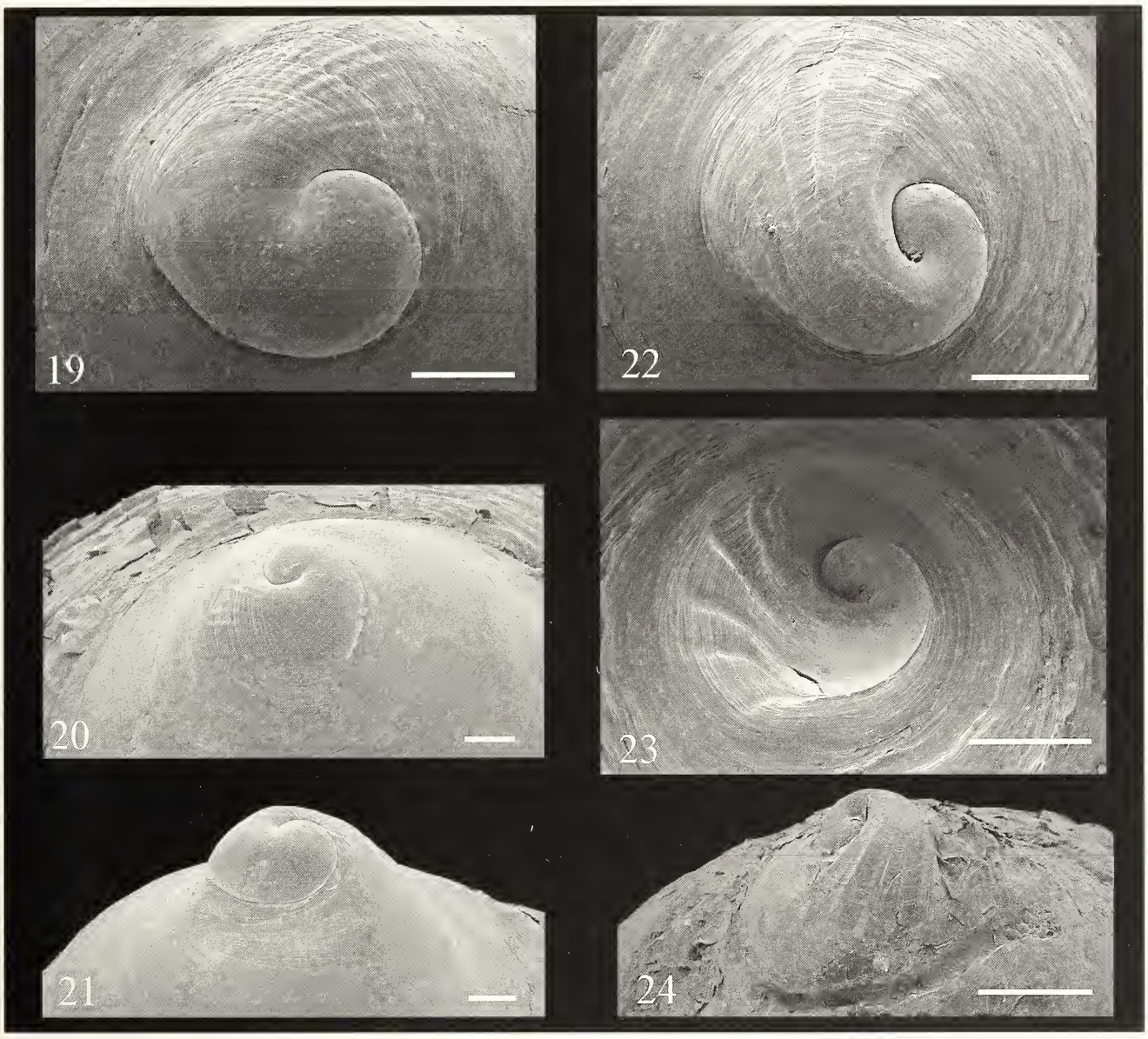
Trochita georgiana Powell, 1951 was described without no mention or comparison with *T. pileolus* (d'Orbigny, 1841). Also, several years later, Powell (1960) in his catalogue of Antarctic and Subantarctic Mollusca neglected again d'Orbigny's species despite the type locality (Malvinas Is. and Patagonian coast) is clearly part of the subantarctic region. The holotype is housed at the NHMUK. Its protoconch and the septum as well as the distribution cited in the original description undoubtedly refer to *T. pileolus*. It is interesting to see that Powell's draw of the holotype (1951: 127, pl. 7, fig. 22) is not covered by bryozoans as it is the real shell and most of *T. pileolus* specimens.

***Trochita pileus* (Lamarck, 1822)**
(Figures 13–18, 19–21, 25–33, 41)

Trochus pileus Lamarck, 1822: 11.
Calyptraea costellata Philippi, 1845: 62; Strebel, 1906: 159, pl. 13, figs. 88–97; Carcelles, 1950: 57; Castellanos, 1970: 41, pl. 3, fig. 9.
?*Trochita corrugata* Reeve, 1859: pl. 2, sp. 9.
Trochita clypeolum Reeve, 1859: pl. 3, sp. 14; Powell, 1951: 127;
Trochita decipiens Rehder, 1943: 44, fig. 2 (non Philippi,1845).



Figures 13–18. *Trochita pileus* (Lamarck, 1822). **13–15.** Syntype of *Trochus pileus* Lamarck, 1822, MHNG INVE 51452/2 (ex 1095/54-2). **16–18.** Probable holotype of *Calyptraea costellata* Philippi, 1845, MNHNS unnumbered. Scale bar = 1 cm.



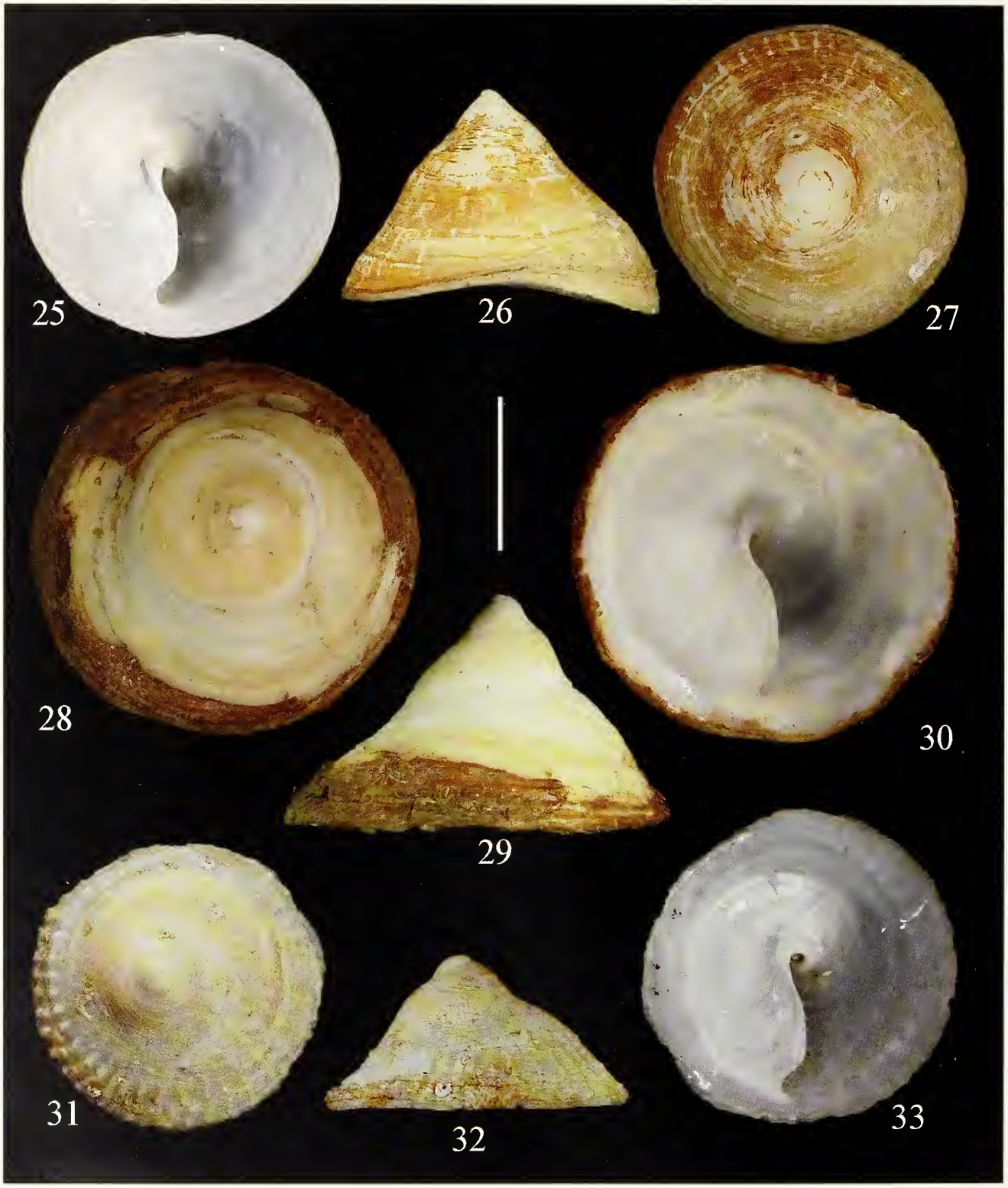
Figures 19–24. *Trochita* species. **19–21**. *Trochita pileus* (Lamarck, 1822). Three views of the protoconch of MACN-In25072, from Bahía Buen Suceso, Tierra del Fuego, Argentina. **22–24**. *Trochita pileolus* (d'Orbigny, 1841). **22**. Protoconch of MACN-In25072-1, from Bahía Buen Suceso. **23–24**. Two views of MACN-In5171 from Ría Santa Cruz. Scale bars = 500 μm.

Trochita trochiformis Powell, 1951: 126, fig. E 2 (non Gmelin, 1791);
Calyptraea pileolus Carcelles, 1950: 57, pl. 2, fig. 25 (non d'Orbigny, 1841). Castellanos, 1970: 40, pl. 3, fig. 5;
Trochita pileus (Lamarck, 1822).—Powell, 1960: 143;

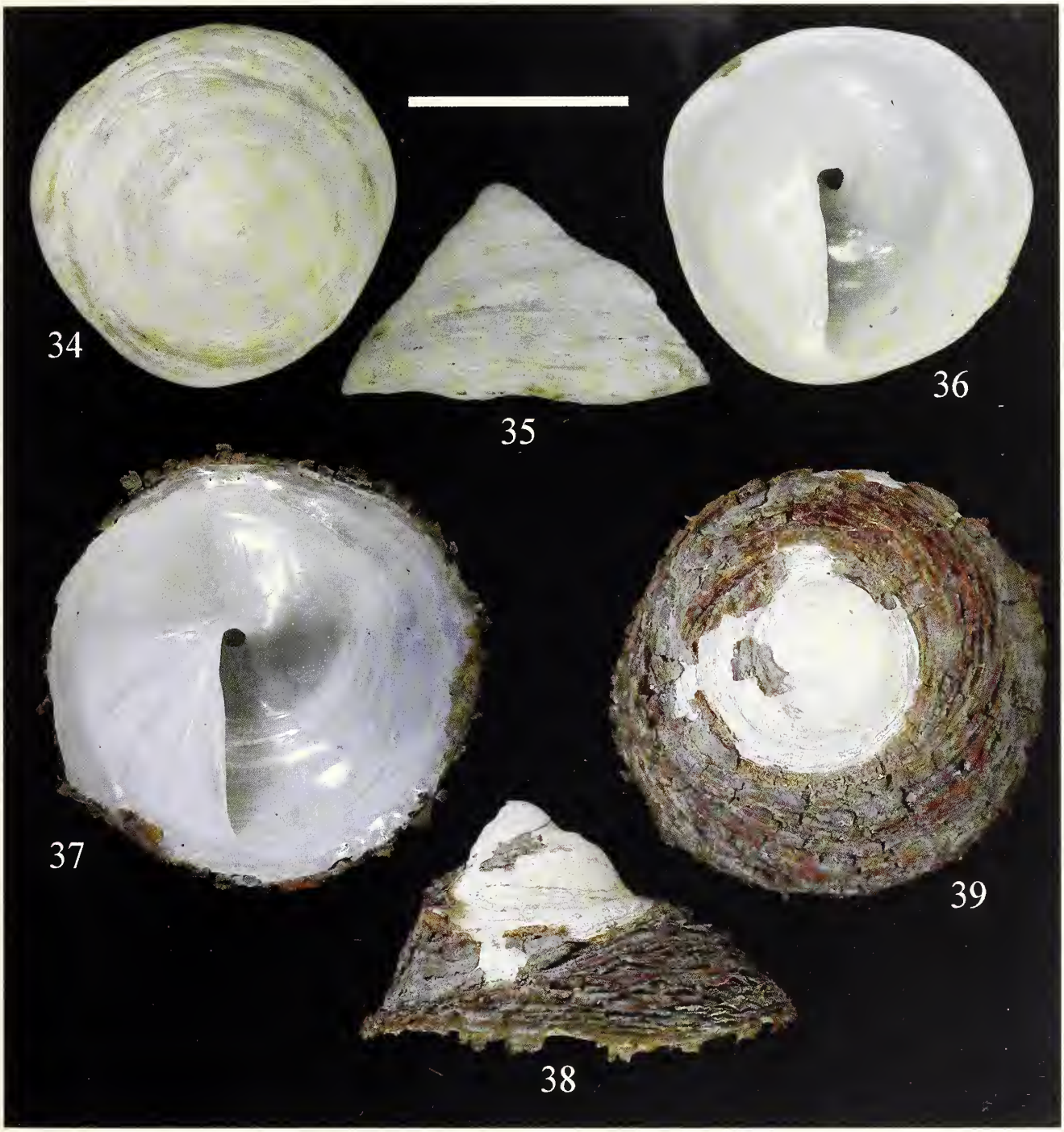
Description: Shell conical, medium size, (H/W=0.56 ±0.08, n=20) circular base of ~3 somewhat flat whorls of about 3 cm of maximum diameter (x=1.74, n=20) and about 1.7 cm of maximum height (x=1.05, n=20); apex central, protoconch prominent of 1.5 whorls, first whorl smooth, later multiple weak spiral threads that cross growth lines and vanished on teleoconch; teleoconch with about 25 thin ribs on the two last whorls, first whorl usually smooth, some specimens with irregular spiral wrinkles only; ribs somewhat scaly when crossing growth lines and continues thru suture to the next whorl. Aperture circular, umbilicus present but sometimes covered by septum; septum sigmoid reflexed on the umbilical area and a sinus on the margin. Periostracum thick, yellow pale, thin, transparent to dark brown.

The radula showed no significant differences from *T. pileolus*.

Type Material: [*Trochus pileus*], three syntypes housed at MHNG INVE 51452/1–3 (old registration number MHNG 1095/54/1–3); [*Calyptraea costellata*], one specimen probable syntype present in MNHNS;



Figures 25–33. *Trochita pileus* (Lamarck, 1822). **25–27**. MACN-In39309, Puerto San Julián, Santa Cruz, Argentina, on the dock pilots. **28–30.** MACN-In 38191, 36°30′S, 54°44′ W. **31–33.** MACN-In22873, Puerto Parry, Isla de los Estados, Argentina. Scale bar = 1 cm.

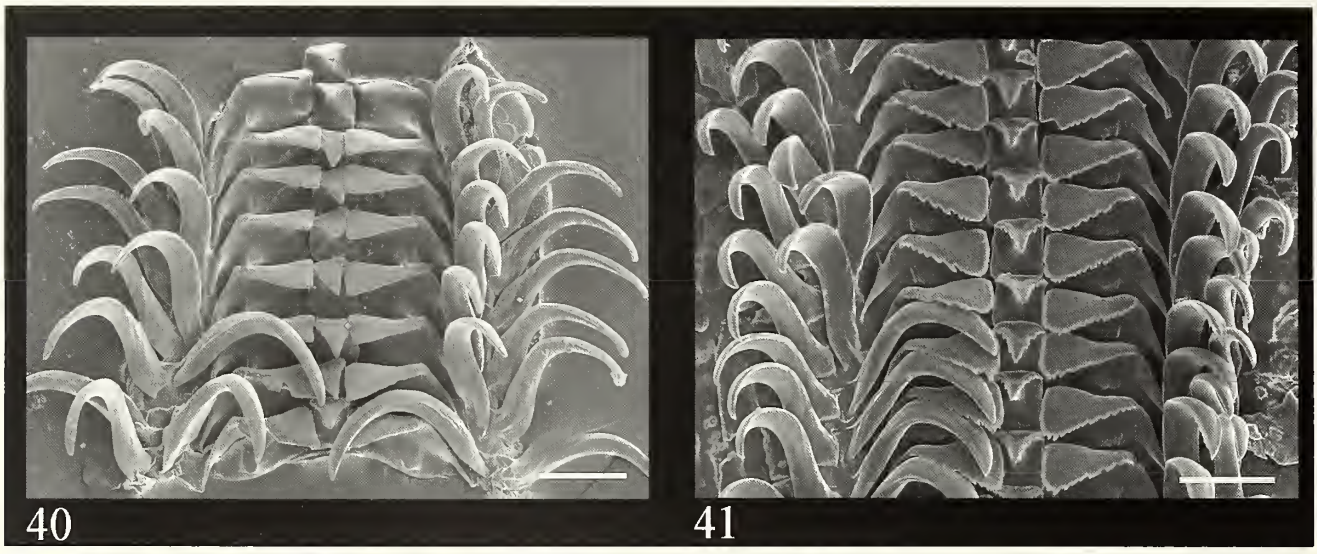


Figures 34–39. *Trochita pileolus* (d'Orbigny, 1841). **34–36.** MACN-In12541 from Punta Sinaia, Tierra del Fuego. **37–39.** MACN-In18969, Bahía Cumberland, South Georgia Is. Argentina. Scale bar = 1 cm.

[*Trochita corrugata*], 3 syntypes housed at NHMUK 1977148 (not seen) [*Trochita clypeolum*] holotype NHMUK 1977149 (not seen).

Type Locality: [*Trochus pileus*] unknown, however, there is a written label, not from Lamarck's, stating Antilles? (Y. Finet, Com. Pers.); [*Calyptraea costellata*] "*frctum magellanicum*"; [*Trochita corrugata*] "Callao, Peru"; [*Trochita clypeolum*] "Straits of Magalhaens".

Other Material Examined: Argentina: 36°30′ S, 54°44′ W, 1 sp. in 26 m, MACN-In 38191; 37°40′ S, 56°25′ W, 1 sp., MACN-In15805; Puerto Quequén, 6 sp., MACN-In 22921; 38°31′ S, 55°42′ W, 13 sp. in



Figures 40–41. Radulae of *Trochita* species. **40.** *Trochita pileolus*, MACN-In36293, 53°58′ S, 37°09′ W. **41.** *Trochita pileus* MACN-In39309. scale bars = 100 µm.

109 m, MACN-In 23358; 38°18′38″ S, 56°58′59.4″ W, in 66 m, St. 5, B/I Puerto Deseado, 9 sp, MACN-In39311; 38°25′ S, 56°30′ W, 1 sp., MACN-In30496; 38°46′53″ S, 55°50′30″ W, in 97 m, St. 7 B/I Puerto Deseado, 8 sp., MACN-In39310; 38°50′56″ S, 55°39′08″ W, in 114 m, St. 8 B/I Puerto Deseado, 16 sp. MACN-In39308; 39°01′40″ S, 58°10′40″ W, in 55 m, St. 11 B/I Puerto Deseado, 1 sp. MACN-In39301; 39°12′ S, 56° W, in 110–128 m, MACN-In20846; 39°00′ S, 57°10′ W, 1 sp. in 177–82 m, MACN-In15225-1; South of Quequén, 2 sp., MACN-In26290; 40°03′ S, 57° W, 2 sp. in 91 m, MACN-In15689; 41°12′ S, 62°54′ W, 2 sp. in 27 m, MACN-In20655; 42°22′02″ S, 63°11′52.6″ W, St. 11, B/I Puerto Deseado, in 63 m, 1 sp., MACN-In39302; Punta Norte, Península Valdés, several sp., MACN-In11480; North of Puerto Madryn, Chubut, 1 sp., MACN-In29643; Rawson, mouth of Rio Chubut, 1 sp., MACN-In10718; Bahía Cruz, Chubut, I sp., MACN-In9014-1; 44°16′ S, 65°12′ W, Bahía Vera, 6 sp, in 46 m, MACN-In23745; 45°00′25.1″ S, 65°16′44.2″ W, St. 9, B/I Puerto Deseado, in 85/89 m, 13 sp., MACN-In39312; 45° S, 65°32′ W, 1 sp. in 86 m, MACN-In24097; 45°08′ S, 66°28′ W, 3 sp., MACN-In23842; 45°09′S, 66°27′ W, 77 sp. in 15 m, MACN-In23809; 45°15′ S, 65°26′ W, 1 sp., in 97 m, MACN-In9151; Dos Hermanas, Puerto Deseado, Santa Cruz, 8 sp., MACN-In26188; Punta Cavendish, Puerto Deseado, 1 sp., MACN-In26185; Isla Quiroga, Ría de Puerto Deseado, 7 sp., intertidal, MACN-In35614; Río Deseado, 2 sp., in 16 m, MACN-In14970; Río Deseado, off Baliza Alianza, 2 sp., in 4 m, MACN-In14971; Ría Deseado, 2 sp., 6 m, MACN-In14973; Bahia Uruguay, Puerto Deseado, 21 sp., MLP266; Puerto Deseado, Santa Cruz, 16 sp., MACN-In17746; 2 sp., MLP261; 9 sp., MLP4748; 1 sp., MLP4785-2 and 18 sp., MLP3892; Punta Medanosa, Santa Cruz, 2 sp., MLP259; Cabo Blanco, Santa Cruz, 2 sp., MACN-In23623; 47°47′39.9″ S, 65°34′53.9″ W, St. 5, B/I Puerto Deseado, in 46 m, 23 shells, 18 sp., MACN-In39313; Cabo Blanco, Santa Cruz, 15 sp., MACN-In17745; San Julián, Santa Cruz, 5 sp., MACN-In 9200; San Julián, 2 sp, MACN-In9237; Puerto San Julián, on the dock pilots, Santa Cruz, 15 sp. in 1–2 m, MACN-In39309; Punta Peña beach, San Julián, Santa Cruz, 64 sp., MLP3024; Ria Santa Cruz, 7 sp., MACN-In5171; Bahía Buen Suceso, Tierra del Fuego, 9 sp., MACN-In25072; 54°28′58.5″ S, 64°57′24.6″ W, St. 1, B/I Puerto Deseado, in 106 m, 62 shells, 1 sp. MACN-In39314; 54°25′ S, 65°49′ W, 1 sp., MLP4350; Puerto Parry, Isla de los Estados, 10 sp. MACN-In22873; Puerto Parry, Isla de los Estados, 10 sp., MACN-In22874; Puerto San Juan, Isla de los Estados, 2 sp., MACN-In22160; Puerto Roca, Isla de los Estados, 2 sp. in 18 m, MACN-In21982; Puerto Cook, Isla de los Estados, 14 sp., MACN-In22093; Puerto Cook, 2 sp., MACN-In22094; Puerto Roca, Isla de los Estados, 2 sp., MACN-In21982; Puerto Olla, Isla Observatorio, 2 sp. in 18–36 m, MACN-In22037; Punta Colnett, Isla de los Estados, 2 sp., MACN-In22566; Rio del Fuego, Tierra del Fuego, 16 sp., MACN-In12539; Río Grande, Tierra del Fuego, 13 sp., MACN-In12540; Punta Sinaia, Tierra del Fuego, 21 sp. MACN-In12357-1; Cabo Santa Inés, Tierra del Fuego, 3 sp., MACN-In12538; Tierra del Fuego, 1 sp., MACN-In20496; Tierra del Fuego, 3 sp., MACN-In21157-1; Canal Beagle, Tierra del Fuego, 1 sp., MLP260; Islas Malvinas (Falklands Is.) 3 sp., MACN-In10152; 51°46′ S, 68°45′ W, 68 sp. in 22 m, MACN-In23858-1; 52°22′ S, 68°29′ W, several sp., in 18 m, MACN-In24061; 53°6′ S, 67°4′1.1 W, in 37–46 m 1 sp. USNM896262; 53°6′ S, 67°4′1.1W, in 86 m 2 sp. USNM896261; 54°50′ S, 64°01′ W, 4 sp. in 154 m, MACN-In22734; 54°27′ S, 63°35′ W, 2 sp., MACN-In22292; 54°26′30″ S, 64°53′ W, 6 sp. in 112 m, MACN-In25025; 54°41′S, 64°01′17″ W, in 55 m,

MACN-In22613; Ushuaia, Tierra del Fuego, 1 sp., MACN-In 21157; Ushuaia, 5 sp., MLP4962; Patagonian coasts, 1 sp., MACN-In9237-1; 54°4′58.7″ S, 58°52′1.1″ W, Burdwood Bank, 1 sp. in 119 m, USNM881885; 55°41′ S, 66°34′ W, 15 sp. in 115m, MACN-In24980. Chile: Bahía Lomas, Isla Dawson, 7 sp., MACN-In12461; Bahía Lomas, Isla Dawson, 2 sp., MACN-In12460; Puerto Harris, Isla Dawson, 6 sp., MACN-In12431; Puerto Harris, Isla Dawson, 5 sp., MACN-In12432; Puerto Harris, Isla Dawson, several sp., MACN-In12482; Puerto Harris, Isla Dawson, 5 sp., MACN-In14000; Isla Nueva, 11 sp., MACN-In24957.

Distribution: Off Buenos Aires province (~36° S), Patagonian coast, Isla de los Estados, Islas Malvinas, Straits of Magellan, Tierra del Fuego, Burdwood Bank in the Atlantic, Isla Dawson, Puerto Harris in the Pacific.

Remarks: *Trochita pileus* is a common species living subtidally on hard substrate. The costulate form was confused with *T. trochiformis* but the radial ribs, normally absent, when present are thinner. The septum margin is sigmoid and in the beginning is reflexed while in *T. trochiformis* it is straighter and sharper. In addition, the latter species has a thicker shell and larger apertural diameter and height. The radula of both species is also somewhat different, while *T. pileus* has no denticles on the two marginal teeth, *T. trochiformis* has several.

DISCUSSION

According to the results presented here only two species of the genus *Trochita* are living in the Southwestern Atlantic waters: *T. pileolus* (d'Orbigny, 1841) and *T. pileus* (Lamarck, 1822). Both species have a similar distribution, however while *T. pileus* is quite common and subtidal in the northern part of the distribution, *T. pileolus* is somewhat rare and usually lives deeper. Representatives of the genus could be found from Patagonian deposits of probably Miocene age. Ihering (1907: 148) already mentioned the presence of several species of *Trochita* included what he identified as *T. pileus* from Cenozoic deposits. A complete revision of the Neogene species of *Trochita* could show that the same species are living since that age in Patagonia.

Contrary to other species of *Trochita* (i.e., *T. dhofarensis* and *T. trochiformis* sensu Taylor and Smythe, 1985), the Atlantic species are apparently not related with upwelling areas.

ACKNOWLEDGMENTS

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LITERATURE CITED

Born, I. 1778. Index rerum naturalium musei caesarei vindobonensis Part I Testacea. Vienna, 458 pp.

Cañete, J.I. and R.P. Ambler. 1992. Desarrollo intracapsular del gastrópodo comestible *Calyptraea (Trochita) trochiformis* (Born, 1778), en Chile. Revista Chilena de Historia Natural 65: 255–266.

Cañete, J.I., C. Gallardo, M. Romero, and R.P. Ambler. 2007. Planktonic drifting dispersal of early juvenile *Trochita calyptraeaformis* Born 1778 [Gastropoda: Calyptraeidae]. Journal of Experimental Marine Biology and Ecology 346: 1–7.

Carcelles, A. 1950. Catálogo de los moluscos marinos de Patagonia. Anales del Museo Nahuel Huapi, 2 extra nueva serie 8, 41–100.

Castellanos, Z.J.A. de. 1970. Catálogo de los moluscos marinos bonaerenses. Anales de la Comisión de Investigaciones Científicas de la provincia de Buenos Aires, 8: 9–365.

Collin, R. 2003a. The utility of morphological characters in gastropod phylogenetics: an example from the Calyptraeidae. Biological Journal of the Linnean Society 78: 541–593.

Collin, R. 2003b. Worldwide patterns in mode of development in calyptraeid gastropods. Marine Ecology Progress Series 247: 103–122.

Collin, R. 2003c. Phylogenetic relationships among Calyptraeid gastropods and their implications for the biogeography of marine speciation. Systematic Biology 52: 618–640.

Duncan, F.M. 1937. On the dates of publication of the Society's "Proceedings," 1859–1926. Proceedings of the Zoological Society of London A107(1): 71–84.

Forbes, E. 1850. [1852]. On the marine mollusca discovered during the voyages of the Herald and Pandora, by Capt. Kellett, R.N., and Lieut. Wood, R.N. Proceedings of the Zoological Society of London for 1850: 270–274. (According to Duncan, 1937 this work was published on 1852)

Gmelin, J.F. 1791. Caroli a Linné, Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis. Editio decima tertia, aucta, reformata, cura J. F. Gmelin.: Lipsiae, Georg. Emanuel. Beer, 3021–3910 pp.

Ihering, H. von. 1907. Les Mollusques fossiles du Tertiaire et du Cretace superieur de l'Argentine. Anales del Museo Nacional de Buenos Aires. Serie III: 1–611.

Keen, M. 1971. Seashells of Tropical West American. Stanford, California, Stanford University Press, 1064 pp.

Knorr, G.W. 1760–1773. Les delices des yeux et de l'esprit, ou collection generale des differentes especes de coquillages que la mer enferme communiquee au public par les heritiers de George Wolfgang Knorr. Nuremberg.

Lamarck, J.B.P.A.d.M.d. 1809. Philosophie Zoologique. vol. 1, Dentu, Paris, 428 p.

Lamarck, J.B.P.A.d.M.d. 1816. Tableau encyclopédique et méthodique des trois règnes de la nature, vingt-troisime partie, Mollusques et Polypes divers. Paris, chez Mme. Veuve Agasse, 391–488, 16 pl.

Lamarck, J.B.P.A.d.M.d. 1815–1822. Histoire Naturelle des animaux sans vértebrés. Paris.

Marincovich, L. 1973. Intertidal mollusks of Iquique, Chile. Bulletin of the Natural History Museum of Los Angeles County 70: 1–49.

Nicklès, M. 1950. Mollusques testacés marins de la côte occidentale d'Afrique: Manuels Ouest-Africains, 2, 269, 464 pp.

Orbigny, A.D. d' (1834–1847) Mollusques, in Bertrand, C.P., ed., Voyage dans l'Amerique Meridionale (Le Bresil, La Republique Orientale de L'Uruguay, La Republique Argentine, La Patagonie, La Republique du Chili, La Republique de Bolivia, La Republique du Perou), execute pendant les annees 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833, 5 (3). Paris, Chez Ve. Levrault, 758 pp.

Paredes, C. and F. Cardoso. 2007. La Familia Calyptraeidae en el Perú (Gastropoda: Caenogastropoda). Revista Peruana de Biología, número especial 13: 177–184.

Pastorino, G. 2005. Recent Naticidae (Mollusca: Gastropoda) from the Patagonian coast: The Veliger 47: 225–258.

Philippi, R.A. 1845. Diagnosen einiger neuen conchylien. Archiv fur Naturgeschichte 11: 50–71.

Powell, A.W.B. 1951. Antarctic and subantarctic mollusca: Pelecypoda and Gastropoda: Discovery Reports 26: 47–196.

Powell, W.B. 1960. Antarctic and subantarctic mollusca. Records of the Auckland Institute and Museum 5: 117–193.

Reeve, L. 1843–1878. Conchologia Iconica: or, illustrations of the shells of moluscous animals.

Rehder, H.A. 1943. The molluscan genus *Trochita* Schumacher with a note on Bicatillus Swainson. Proceedings of the Biological Society of Washington 56: 41–46.

Reid, D.G. and C. Osorio. 2000. The shallow-water marine mollusca of the Estero Elefantes and Laguna San Rafael, southern Chile. Bulletin of the Natural History Museum of London (Zoology) 66: 109–146.

Sowerby, G.B., I. 1839. In: J. E. Gray, Molluscous Animals. In: The Zoology of Captain Beechey's Voyage; compiled from the collections and notes made by Captain Beechey, the officers and naturalist of the expedition, During a voyage to the Pacific and Behring's Straits performed in his Majesty's ship Blossom, under the command of Captain F. W. Beechey, in the years 1825, 26, 27 and 28.Volume 1. H. G. Bohn, London. pp. 143–155, pls. 33–44.

Schumacher, C.F. 1817. Essais d'un nouveau système des habitations des vers testacès. Copenhagen, 287 pp.

Strebel, H. 1906. Beiträge zur Kenntnis der Molluskenfauna der Magalhaen-Provinz. 4: Zoologischen Jahrbuchern. Abteilung fur Systematik, Geographie und Biologie der Tiere 24: 91–174.

Taylor, J.D. and K.R. Smythe. 1985. A new species of *Trochita* (Gastropoda: Calyptraeidae) from Oman: a relict distribution and association with upwelling areas. Journal of Conchology 32: 39–48.

Tryon, G.W.J. 1886. Manual of Conchology structural and systematic with illustrations of the species. Naticidae, Calyptraeidae, Turritellidae, Vermetidae, Caecidae, Eulimidae, Turbonillidae, Pyramidellidae. Philadelphia, 461 pp.

Vokes, E.H. 1975. Some new or otherwise interesting members of the Calyptraeidae (Mollusca: Gastropoda). Tulane Studies in Geology and Paleontology 11: 163–172.

Zelaya, D. 2005. Systematics and biogeography of marine gastropod molluscs from South Georgia. Spixiana 28: 109–139.

Two Neogene vesicomyid species (Bivalvia) from Japan and their biogeographic implications

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ABSTRACT

A new species of the bivalve family Vesicomyidae, *Calyptogena veneriformis*, is described from the Pliocene part of the Kurokura Formation in Niigata Prefecture, Japan. This species belongs to the Plio-Pleistocene Omma-Manganji fauna on the coast of the Japan Sea. We document previously unknown characters of the shell interior of *"Vesicomya" kawadai* (Aoki) from lower to middle Miocene deposits in Honshu, Japan, showing that the species belongs to the genus *Pliocardia*. The genus *Pliocardia* might have a longer geologic history than previously appreciated. When the currently known distribution of *Pliocardia* is taken at face value, the genus might have colonized the Atlantic Ocean only very recently, perhaps as late as the Pliocene, despite its long geologic history.

Additional keywords: Pliocardia, Vesicomya, Calyptogena, Plio-Pleistocene

INTRODUCTION

The Vesicomyidae is one of the six bivalve families living in symbiosis with chemoautotrophic bacteria, with a geologic history ranging back to the middle Eocene (Taylor and Glover, 2010; Kiel, 2010). Due to the limited number of shell characters and the high morphologic plasticity among the vesicomyids, Japanese malacologists often subdivided the family into two genera, *Calyptogena* Dall, 1891 for large elongate shells, and *Vesicomya* Dall, 1886 for small subcircular or veneriform shells (e.g. Sasaki et al., 2005). Recently, we have examined fossil representatives of large, elongate vesicomyids in the northern Pacific region (Amano and Kiel, 2007, 2010, 2011; Kiel and Amano, 2010) and distinguished four genera: *Calyptogena*, *Archivesica* Dall, 1908, *Adulomya* Kuroda, 1931, and *Hubertschenckia* Takeda, 1953.

The genus *Calyptogena* is composed of ten or more Recent species (Krylova and Sahling, 2006, 2010). Among them, only one species, *Calyptogena pacifica* Dall, 1891, has fossil representatives, ranging from the upper Miocene to the middle Pleistocene in the Japan Sea Borderland (Kanno et al., 1989; Amano, 2003; Amano and Kanno, 2005; Amano and Jenkins, 2011). We have now recovered one new species of *Calyptogena* from the Japan Sea borderland, from the lower Pliocene part of the Kurokura Formation in Niigata Prefecture.

Among the small vesicomyids (*"Vesicomya"* of Japanese malacologists), Cosel and Salas (2001) recognized several genera, namely *Vesicomya*, *Isorropodon* Sturany, 1896, *Waisiuconcha* Beets, 1942, and *Callogonia* Dall, 1889. In addition, Krylova and Janssen (2006) and Krylova and Sahling (2010) redefined the small vesicomyid genus *Pliocardia* Woodring, 1925, and included two Japanese species, *Vesicomya crenulomarginata* Okutani, Kojima, and Iwasaki, 2002 and *V. kuroshimana* Okutani, Fujikura and Kojima, 2000. According to these taxonomic revisions, the genus *Vesicomya* is now confined to very small species (3–13 mm long) having subcircular shells and thin cardinal teeth that are arranged roughly in a linear fashion. Three fossil species were reported as *"Vesicomya"* from Cretaceous and Neogene deposits in Japan: *Vesicomya kawadai* (Aoki, 1954), *V. inflata* Kanie and Nishida, 2000, and *V. ellipsoidea* Kanie and Kuramochi, 2001. Among them, Amano et al. (2008) showed that *V. inflata* from Cretaceous deposits in Hokkaido is a lucinid, not a vesicomyid, and established the new genus *Ezolucina* for this species. *"Vesicomya" ellipsoidea* has a large and elongate shell (up to 188.6 mm long) and two cardinal teeth in right valve and does therefore belong to *Archivesica* or *Adulomya* rather than *Vesicomya sensu stricto* (Amano and Kiel, 2011). The generic status of *Vesicomya kawadai* has so far remained uncertain.

The scope of the present contribution is (1) to describe and name the new species of *Calyptogena*, (2) to clarify the generic status of *"Vesicomya" kawadai* based on newly collected material, and (3) to discuss the biogeographic significance of these species.

MATERIALS AND METHODS

Several small vesicomyid specimens were recovered from calcareous concretions within the mudstone of the

lower Pliocene part of the Kurokura Formation at Sugawa in Joetsu City, Niigata Prefecture (Figure 1, Loc. 1), and they occur in association with *Calyptogena pacifica* Dall, 1891 and the thyasirid bivalve *Conchocele bisecta* (Conrad, 1849). These specimens are described as *Calyptogena veneriformis* herein.

The specimens of *"Vesicomya" kawadai* examined herein are from the type locality of this species, in the lower Miocene Honya Formation at Donosaku in Iwaki City, Fukushima Prefecture (Figure 1, Loc. 2). The specimens were found in a large calcareous concretion where they co-occur with *Adulomya chitanii* Kanehara, 1937 and *Conchocele bisecta*. Some specimens of *"Vesicomya" kawadai* from the Honya Formation in the Ishimoriyama area of Iwaki City, Fukushima Prefecture (Figure 1, Loc. 3) were examined. These specimens were collected by the late Prof. Katsumi Hirayama of Rikkyo University, and the exact locality and the associated fauna are unknown. In addition, two specimens of *"Vesicomya" kawadai* were collected on the Rekifune River (Figure 1, Loc. 4), about 400 m downstream from the fossil whale-fall site described by Amano et al. (2007), in eastern Hokkaido. The specimens were collected from carbonaceous mudstones of the middle Miocene Nupinai Formation, which most likely represent an ancient cold-seep site, inferred from the associated species *Adulomya chitanii*, *Conchocele bisecta*, and *Portlandia* sp.

We also reexamined the specimens of *"Vesicomya" kawadai* described by Amano et al. (2001) from the uppermost lower to lowermost middle Miocene Higashibessho Formation at Shimo-sasahara in Toyama Prefecture (Figure 1, Loc. 5). All specimens are deposited in the Joetsu University of Education (JUE).

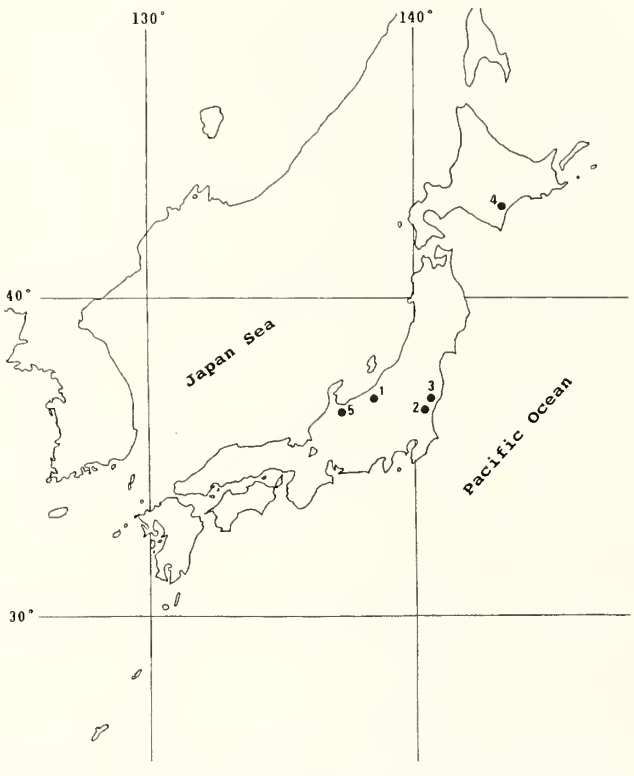


Figure 1. Localities of the fossil vesicomyids described herein. 1: Sugawa in Joetsu City, Niigata Pref. (lower Pliocene). 2: Donosaku in Iwaki City, Fukushima Pref. (lower Miocene); 3: Ishimoriyama area of Iwaki City, Fukushima Pref. (lower Miocene). 4: Rekifune River, Hokkaido (middle Miocene). 5: Shimo-sasahara, Toyama Prefecture (uppermost lower to lowermost middle Miocene). *Calyptogena veneriformis* was collected from Loc. 1. *Pliocardia kawadai* was recovered from Locs. 2–5.

SYSTEMATICS

Family Vesicomyidae Dall and Simpson, 1901
Subfamily Pliocardiinae Woodring, 1925

Genus *Pliocardia* Woodring, 1925

Type Species: *Anomalocardia bowdeniana* Dall, 1903 from the upper Pliocene Bowden Formation in Jamaica; by original designation.

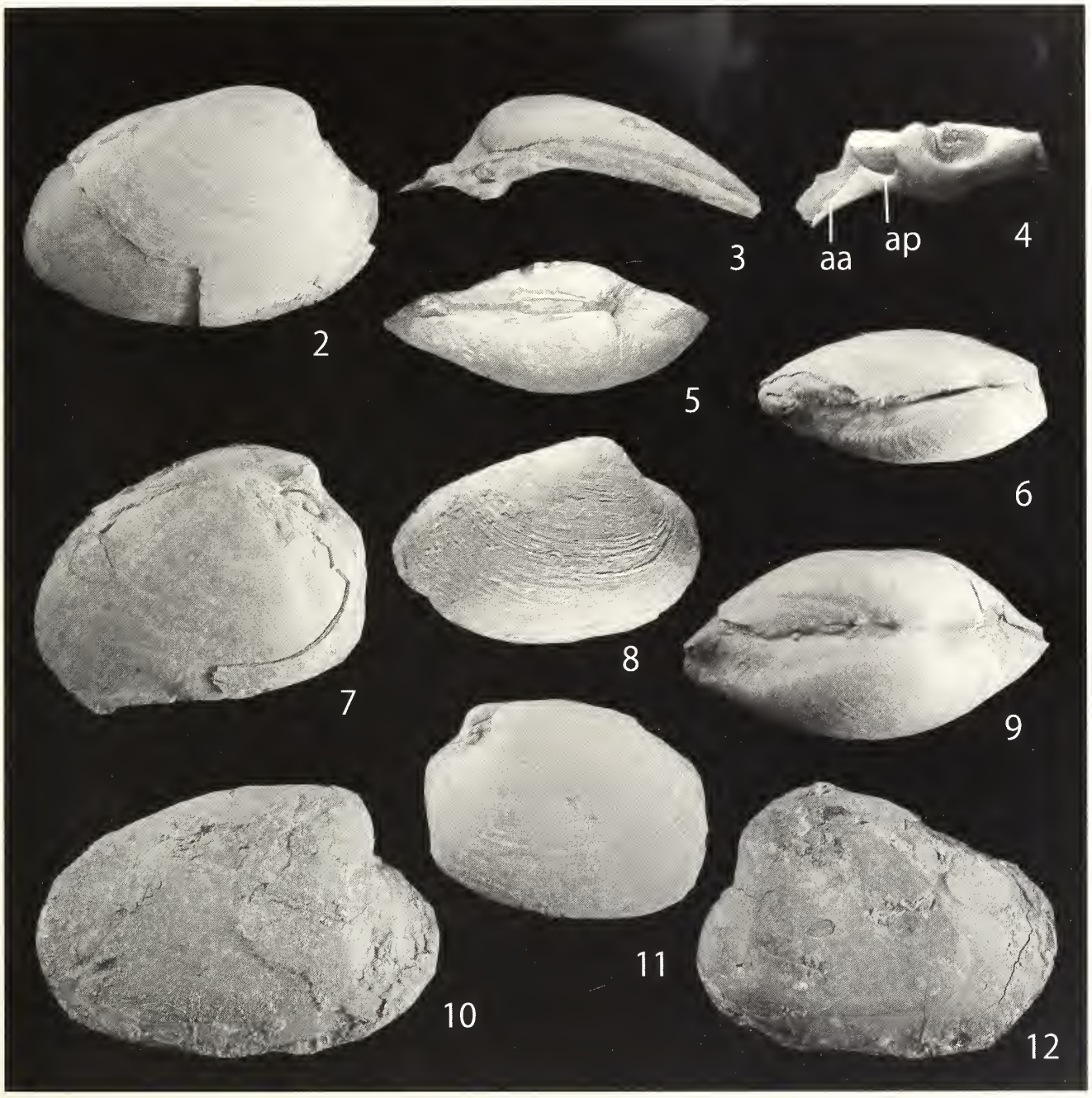
Remarks: According to the redefinition by Krylova and Janssen (2006), this genus is characterized by its small- to medium-sized elliptical shells having a shallow radial depression from beak to postero-ventral margin, a deep lunular incision, a shallow pallial sinus and a stout ventral tooth (1) overlying the subumbonal cardinal teeth (3a, 3b) in the right valve.

Pliocardia kawadai (Aoki, 1954)
(Figures 2–4, 6–7, 9–12)

Lamelliconcha kawadai Aoki, 1954: 36–37, pl.2, figs.1, 10, 12–15, 22.
Vesicomya kawadai (Aoki).—Kamada, 1962: 88–89, pl.8, figs. 2a–b; Amano et al., 2001: 192, figs. 3–5, 8–11; Amano et al., 2007: figs. 3D, E, G, J.

Description: Shell thin, medium sized (up to 40.7 mm long), ovate, with radial depression extending from beak to postero-ventral corner, with distinct, shallow lunular incision. Pallial sinus shallow and v-shaped, situated just before radial inner ridge extending from beak to posterior corner. On hinge of right valve, ventral tooth (1) thin to moderately thick, overlain by arched subumbonal teeth (3a, 3b); cardinal tooth 3b bifid in some specimens. Left valve hinge with thin cardinal tooth 2a and stout cardinal tooth 2b, connected with a thin tooth 4b. Anterior adductor muscle scar ovate with rather straight and sharp posterior margin; anterior pedal retractor scar with semi-circular shape, deeply impressed with rough striations subparallel to shell margin, located between hinge plate and anterior adductor muscle scar, from which it is separated by a sharp step. Posterior adductor muscle scar ovate or circular and deeply depressed.

Material Examined: Twenty-seven specimens: JUE nos. 15895, 15896, 15897.



Figures 2–12. *Pliocardia* species. **2–4, 6–7, 9–12.** *Pliocardia kawadai* (Aoki). **2, 3.** Right valve surface and hinge. Length 40.7 mm, hinge length 22.8 mm, JUE no. 15895-2; Loc. 3. **4.** Anterior pedal retractor scar. Illustrated hinge length 12.7 mm; aa, anterior adductor scar; ap, anterior pedal retractor scar; JUE no.15697; Loc. 5. **6, 11.** Right valve hinge and weak lunule incisa. Length 24.7 mm, JUE no. 15897-1; Loc. 4. **7.** Inner surface of right valve and left valve hinge. Length 32.6mm, JUE no. 15895-3, Loc. 3. **9.** Escutcheon and lunule incisa. Length 35.4 mm, JUE no. 15895-1; Loc. 3. **10.** Right valve. Length 40.0 mm, JUE no. 15896-1; Loc. 2. **12.** Inner surface of left valve. Length 35.4 mm, JUE no. 15896-2; Loc. 2. **5, 8.** *Pliocardia* sp. from an Oligocene seep carbonate in the Lincoln Creek Formation in Washington State, USA (LACMIP loc. 17447B, see Amano and Kiel, 2007 for details). **5.** Dorsal view. **8.** view on right valve showing the posterior radial depression; length 16.0 mm.

Distribution: Lower Miocene Honya Formation in Fukushima Prefecture; uppermost lower to lowermost middle Miocene Higashibessho Formation in Toyama Prefecture; middle Miocene Nupinai Formation in Hokkaido (from both seep and whale-fall sites).

Remarks: As shown by Amano et al. (2001), specimens from the Higashibessho locality (Loc. 5) usually have a stouter ventral tooth in the right valve than the specimens from the type locality of "*Vesicomya*" *kawadai* in the Honya Formation. Based on the hinge dentition of

the right valve, the presence of a lunular incision and the presence of a small pallial sinus, *"Vesicomya" kawadai* is herein transferred to the genus *Pliocardia*.

Comparisons: *Pliocardia kawadai* resembles the Recent species *P. crenulomarginata* (Okutani, Kojima and Iwasaki, 2002) in having a similar hinge dentition in both valves, a radial depressed area from the beak to the postero-ventral corner and a weak ridge before the posterior adductor muscle scar. However, *P. kawadai* differs from *P. crenulomarginata* by having a bifid 3b tooth, no sharply bounded escutcheon and no fine crenulation on the posterior margin.

Similar in outline to *P. kawadai* is a species from a seep carbonate in the upper Oligocene part of the Lincoln Creek Formation in western Washington State, USA (Amano and Kiel, 2007). This species is herein only tentatively assigned to *Pliocardia*. We examined additional specimens from this locality (Figures 5, 8) that show a depressed area running from the beak to the posterior corner and a distinct lunular incision. These features, together with the previously described hinge characters (Amano and Kiel, 2007), confirm the assignment of this species to *Pliocardia*, although the presence or absence of a pallial sinus is unknown. This species is much smaller (16.0 mm long) than the up to 40.7 mm long *P. kawadai*.

Genus *Calyptogena* Dall, 1891

***Calyptogena veneriformis* new species**
(Figures 13–19)

Diagnosis: Small-sized *Calyptogena* with veneriform shell, lunular incision lacking, pallial sinus lacking, subumbonal pit lacking. Middle hinge tooth (1) thin, surrounded by U-shaped connection of anterior (3a) and posterior (3b) teeth in right valve, with posterior nymphal ridge.

Description: Shell up to 19.8 mm in length, rather thin, weakly inflated, triangular veneriform (height/length = 0.73–0.88), equivalve, and inequilateral. Antero-dorsal margin concave, continuing to rounded anterior margin; postero-dorsal margin nearly straight into oblique posterior margin at obtuse angle; ventral margin broadly arcuate. Beak prominent, prosogyrate and located at anterior one-third to two-fifth of shell length (i.e., at 29–45% of shell length from anterior margin). Nymph narrow and short. Lunule and lunular incision absent. Escutcheon very narrow, demarcated and deeply depressed. Surface ornamented with growth lines only. Right valve hinge wide for size, with three cardinal teeth, distinct posterior nymphal ridge and subumbonal pit absent. Posterior tooth of right valve (3b) large and triangular; anterior tooth (3a) short and thin, parallel with dorsal margin and connecting with posterior tooth (3b), forming U-shaped connection; middle tooth (1) long and thin, and surrounded by anterior and posterior teeth. Middle cardinal tooth of left valve (2b) stout, connecting with anteriorly oblique anterior tooth (2a); posterior tooth (4b) thin. Pallial line entire. Anterior adductor scar ovate; posterior adductor scar pear-shaped.

Figures 13–19. *Calyptogena veneriformis* new species. All specimens are from the type locality (Loc. 1). **13–15, 18–19.** Paratypes. **13.** Left valve hinge; hinge length 10.0 mm, JUE no. 15899-5. **14.** Right valve hinge; hinge length 6.6 mm, JUE no. 15899-4. **15.** Right valve hinge; hinge length 10.5 mm, JUE no. 15899-3. **18.** Dorsal view of right valve; length 19.1 mm, JUE no. 15899-1. **19.** Inner structure of right valve; length 12.2 mm, JUE no. 15899-2. **16, 17**. Holotype. **16.** Right valve. **17.** Dorsal view of figure 16; length 11.4 mm, JUE no. 15898. pnr, posterior nymphal ridge; aa, anterior adductor scar; pa, posterior adductor scar.

Holotype: Length, 11.4 mm, height, 9.3 mm, JUE no.15898, right valve.

Paratypes: Length, 19.1 mm, height, 15.1 mm, JUE no. 15899-1, right valve; length, 12.2 mm, height, 10.7 mm, JUE no. 15899-2, right valve; length, 6.2 mm, height, 5.1 mm, JUE no. 15899-6, left valve.

Type Locality: Outcrop at Sugawa, Yasuzuka-ku, Joetsu City, Niigata Prefecture (37°03′41″ N, 138°29′22″ E).

Material Examined: Twenty-two specimens from the type locality (Loc. 1 herein).

Remarks: At its type locality *Calyptogena veneriformis* is associated with *Calyptogena pacifica*. A veneriform shell shape is unknown among the Recent specimens of *C. pacifica*, despite the wide range of variation in shell morphology among Recent *Calyptogena* (Krylova and Sahling, 2006; Krylova and Janssen, 2006; Cosel and Olu, 2009). Furthermore, the morphological variation of fossil *C. pacifica* from the Japan Sea borderland shows narrower range than the Recent one (see Kanno et al., 1989; Amano, 2003; Amano and Kanno, 2005; Amano and Jenkins, 2011). We are therefore confident that *Calyptogena veneriformis* represents a new species independent from *C. pacifica*.

Comparisons: Some specimens of *Calyptogena pacifica* have a veneriform shell similar to that of *C. veneriformis* new species (e.g. Krylova and Sahling, 2006, figure 4, H–M). However, *C. veneriformis* can be distinguished from those specimens of *C. pacifica* by its smaller and triangular shell, and its pear-shaped posterior adductor muscle scar. *Calyptogena veneriformis* is also similar to veneriform specimens of *Calyptogena valdiviae* (Thiele and Jaeckel, 1931) from the Gulf of Guinea as illustrated by Cosel and Olu (2009). However, *C. veneriformis* differs from *C. valdiviae* by having a less inflated and triangular shape. Superficially *C. veneriformis* resembles *Warreniconcha guinensis* (Thiele and Jaeckel, 1931) in its veneriform shell. However, *Warreniconcha guinensis* has a narrower hinge plate than *Calyptogena* and a subumbonal pit, unlike *Calyptogena*.

Calyptogena veneriformis resembles some species currently assigned to *Waisiuconcha* Beets, 1942 (e.g., Cosel and Salas, 2001; Krylova and Janssen 2006; Krylova and Sahling, 2010) in having a similar shell form and left valve hinge dentition. But *C. veneriformis* can be distinguished from *Waisiuconcha* by its broad posterior cardinal tooth (3b) and the U-shaped connection between the posterior and anterior cardinal teeth in the right valve, and by the lack of a lunular incision. However, we urge caution about the currently used concept of *Waisiuconcha* because the type species (*W. alberdinae* Beets, 1942) is known from a single left valve only but the taxonomically informative hinge characters among vesicomyids are usually those of the right valve.

Distribution: Type locality only; lower Pliocene part of the Kurokura Formation in Niigata Prefecture, Japan.

Etymology: Named after its veneriform shell morphology.

DISCUSSION

Krylova and Sahling (2010) identified nine living species of *Pliocardia*, which are found in many basins all over the world ocean (Krylova and Sahling 2010). In addition, there are several undescribed or misidentified extant species in museum collections that are also likely to belong to *Pliocardia* (S. Kiel, personal observation). The fossil history of *Pliocardia* is complicated and requires further research. The Miocene *Pliocardia kawadai* is so far the only fossil representative of this genus in Japan. Apart from *P. kawadai* and the late Pliocene type species, the only other fossil species assigned to *Pliocardia* is an as-yet unnamed species from the Oligocene Lincoln Creek Formation in western Washington State, USA (Amano and Kiel, 2007; see also Figures 5, 8). However, several Paleogene taxa from the North Pacific realm that we have previously identified as *Archivesica* (Amano and Kiel, 2007; Kiel and Amano, 2010), as well as "*Vesicomya*" *tschudi* and "*Vesicomya*" *ramondi* from the Oligocene of Peru (Olsson, 1931), show some marked differences to *A. gigas*, the type species of *Archivesica*. They are all considerably smaller than *A. gigas*, many have a lunular incision, unlike *A. gigas*, and some lack a pallial sinus, unlike *A. gigas*. At least some of these Paleogene taxa may belong to *Pliocardia*, or to new genera. This applies also to the oldest known vesicomyid, "*Archivesica*" cf. *tschudi*, from the middle Eocene Humptulips Formation western Washington State, USA (Amano and Kiel, 2007).

If the currently known distribution of fossil *Pliocardia* is taken at face value, it appears that the genus colonized the Atlantic Ocean only very recently, despite its long geologic history. Whereas the genus is known from the northeastern Pacific at least since the Oligocene and from the northwestern Pacific since the early Miocene, the earliest Atlantic record is the late Pliocene type species *P. bowdeniana*. There are several older seep deposits in the Caribbean region, but *Pliocardia* or *Pliocardia*-like shells were reported from none of them (Gill et al., 2005; Kiel and Peckmann, 2007). On the eastern side of the Atlantic Ocean, several Miocene seep deposits are known from Italy, but again, they seem to lack *Pliocardia* (Taviani, 1994; S. Kiel, personal observation). One likely pathway for the colonization of the Atlantic Ocean by *Pliocardia* is the Isthmus of Panama which closed in the early Pliocene about 4.0–3.5 Ma (e.g. Collins, 1996). A passage through this isthmus was recently suggested by Martin and Goffredi (2011) who found that the closest relative (based on molecular evidence) of "*Pliocardia*" *krylovata* from the Pacific side of Costa Rica is the Caribbean species "*Calyptogena*" *ponderosa* Boss, 1968.

Whereas *Calyptogena pacifica* is widely distributed in late Miocene to middle Pleistocene deposits of the Japan Sea borderland (see Amano and Jenkins, 2011), the new species *Calyptogena veneriformis* is only known from

lower Pliocene deposit in the central part of the Japan Sea borderland. Thus the geologic age of *Calyptogena veneriformis* coincides with the development of the Omma-Manganji fauna (cf., Otuka, 1939; Amano, 2001, 2007). This fauna is endemic for the semi-enclosed Japan Sea and developed after the separation of the Japan Sea from the Pacific Ocean by uplifting of the backbone mountain range in northeastern Honshu (see Iijima and Tada, 1990). *Calyptogena veneriformis* may thus be considered as part of the Omma-Manganji fauna and may have evolved from *C. pacifica*, the only other species of *Calyptogena* present in this basin during the Pliocene.

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LITERATURE CITED

Amano, K. 2001. Pliocene molluscan fauna of Japan Sea borderland and the paleoccanographic conditions. Biological Science (Tokyo) 53: 178–184 (in Japanese).

Amano, K. 2003. Predatory gastropod drill holes in Upper Miocene cold seep bivalves, Hokkaido, Japan. The Veliger 46: 90–96.

Amano, K. 2007. The Omma-Manganji fauna and its temporal change. Fossils (The Palaeontological Society of Japan) 82: 6–12. (in Japanese with English abstract).

Amano, K., T. Hamuro, M. Hamuro, and S. Fujii. 2001. The oldest vesicomyid bivalves from the Japan Sea Borderland. Venus 60: 189–198.

Amano, K. and R. G. Jenkins. 2011. Fossil records of extant vesicomyid species from Japan. Venus 69: 163–176.

Amano, K. and S. Kanno. 2005. *Calyptogena* (Bivalvia: Vesicomyidae) from Neogene strata in the Joetsu District, Niigata Prefecture, central Japan. The Veliger 47: 202–212.

Amano, K. and S. Kiel. 2007. Fossil vesicomyid bivalves from the North Pacific region. The Veliger 49: 270–293.

Amano, K and S. Kiel. 2010. Taxonomy and distribution of fossil *Archivesica* (Bivalvia: Vesicomyidae) in Japan. The Nautilus 124: 155–165.

Amano, K. and S. Kiel. 2011. Fossil *Adulomya* (Vesicomyidae, Bivalvia) from Japan. The Veliger 51: 76–90.

Amano, K., C.T.S. Little and K. Inoue. 2007. A new Miocene whale-fall community from Japan. Palaeogeography, Palaeoclimatology, Palaeoecology 247: 236–242.

Amano, K., R.G. Jenkins, Y. Kurihara, and S. Kiel. 2008. A new genus for *Vesicomya inflata* Kanie and Nishida, a lucinid shell convergent with that of vesicomyids, from Cretaceous strata of Hokkaido, Japan. The Veliger 50: 255–262.

Aoki, S. 1954. Mollusca from the Miocene Kabeya Formation, Joban coal-field, Fukushima Prefecture, Japan. Science Reports of the Tokyo Kyoiku Daigaku, Section C, 3: 23–41.

Beets, C. 1942. Beiträge zur Kenntnis der angeblich oberoligocänen Mollusken-Fauna der Insel Buton, Niederländisch-Ostindien. Leidsche Geologische Mededeelingen 13: 255–328.

Collins, L.S. 1996. Environmental changes in Caribbean shallow waters relative to the closing Tropical American Seaway. In: Jackson, J.B.C., A.F. Budd and A. G. Coates (eds.) Evolution and environment in Tropical America: 130–167.

Conrad, T.A. 1849. Fossils from northwestern America (fossil shells of Astoria, Oregon). In, Dana, J.D. Geology of the United States exploring expedition...under Charles Wilkes 20: 723–728.

Cosel, R. von and K. Olu. 2009. Large Vesicomyidae (Mollusca: Bivalvia) from cold seeps in the Gulf of Guinea off the coasts of Gabon, Congo and northern Angola. Deep-Sea Research II 56: 2350–2370.

Cosel, R. von and C. Salas. 2001. Vesicomyidae (Mollusca: Bivalvia) of the genera *Vesicomya*, *Waisiuconcha*, *Isorropodon* and *Callogonia* in the eastern Atlantic and the Mediterranean. Sarsia 86: 333–366.

Dall, W.H. 1886. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey steamer "Blake", Liet.-Commander C. D. Sigsbee, U.S. N., and Commander J. R. Bartlett, U.S.N., commanding XXIX. Report on the Mollusca, Part 1, Brachiopoda and Pelecypoda. Bulletin of the Museum of Comparative Zoology at Harvard University 12: 171–318.

Dall, W.H. 1889. Reports on the Mollusca, pt.2. Gastropoda and Scaphopoda. Reports on the dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey steamer "Blake". Bulletin of the Museum of Comparative Zoology at Harvard University 18: 1–492.

Dall, W.H. 1891. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. XX. On some new or interesting West American shells obtained from dredgings of the U.S. fish commission steamer Albatross in 1888. Proceedings of the U.S. National Museum 14: 174–191.

Dall, W. H. 1903. Contributions of the Tertiary fauna of Florida with especial reference to the Silex Beds of Tampa and the Pliocene beds of Caloosahatchie River, including in many cases a complete revision of the generic groups treated of and their American Tertiary species. Part VI. Concluding the work. Transactions of the Wagner Free Institute of Science of Philadelphia 3: 1219–1654.

Dall, W.H. 1908. Reports on the dredging operations off the west coast of Central America ... The Mollusca and Brachiopoda. Bulletin of the Museum of Comparative Zoology at Harvard University 43: 205–487.

Dall, W.H. and C.T. Simpson. 1901. The Mollusca of Porto Rico. Bulletin of the United States Fish and Fisheries Commission 20: 351–524.

Gill, F.L., I.C. Harding, I.C., C.T.S. Little, and J.A. Todd. 2005. Palaeogene and Neogene cold seep communities in Barbados, Trinidad and Venezuela: An overview. Palaeogeography, Palaeoclimatology, Palaeoecology, 227: 191–209.

Iijima, A. and R. Tada. 1990: Evolution of Tertiary sedimentary basins of Japan in reference to opening of the Japan Sea. Journal of the Faculty of Science, the University of Tokyo, Section 2 22: 121–171.

Kamada, Y. 1962. Tertiary marine Mollusca from the Joban coal-field, Japan. Special Papers, Palaeontological Society of Japan 8: 1–187.

Kanehara, K. 1937. Miocene shells from the Joban coal-field. Bulletin of the Imperial Geological Survey of Japan 27: 1–12.

Kanie, Y., and T. Kuramochi. 2001. Two new species of the Vesicomyidae (Bivalvia: Mollusca) from the Pliocene Shiramazu Formation of the Chikura Group in the Boso Peninsula, Japan. Science Reports of the Yokosuka City Museum 48: 1–9. [in English with Japanese abstract]

Kanie, Y. and T. Nishida. 2000. New species of chemosynthetic bivalves, *Vesicomya* and *Acharax*, from the Cretaceous deposits of northwestern Hokkaido. Science Report of the Yokosuka City Museum 47: 79–84.

Kanno, S., K. Amano, and H. Ban. 1989. *Calyptogena* (*Calyptogena*) *pacifica* Dall (Bivalvia) from the Neogene system in the Joetsu district, Niigata prefecture. Transactions and Proceedings of the Palaeontological Society of Japan, New Series 153: 25–35.

Kiel, S. 2010. The fossil record of vent and seep mollusks. In: Kiel, S. (ed.). The vent and seep biota, Topics in Geobiology 33: 255–277.

Kiel, S. and K. Amano. 2010. Oligocene and Miocene vesicomyid bivalves from the Katalla district in southern Alaska, USA. The Veliger 51: 76–84.

Kiel, S. and J. Peckmann. 2007. Chemosymbiotic bivalves and stable carbon isotopes indicate hydrocarbon seepage at four unusual Cenozoic fossil localities. Lethaia, 40: 345–357.

Krylova, E.M. and R. Janssen. 2006. Vesicomyidae from Edison Seamount (South Western Pacific: Papua New Guinea: New Ireland fore-arc basin) (Bivalvia: Glossoidea). Archiv für Molluskenkunde 135: 233–263.

Krylova, E.M. and H. Sahling. 2006. Recent bivalve molluscs of the genus *Calyptogena* (Vesicomyidae). Journal of Molluscan Studies 72: 359–395.

Krylova, E.M. and H. Sahling. 2010.Vesicomyidae (Bivalvia): Current taxonomy and distribution. PloS ONE 5 (4): 1–9.

Kuroda, T. 1931. Fossil Mollusca. In: Homma, F. (ed.). Geology of the central part of Shinano, part 4. Kokin Shoin, Tokyo: 1–90 [in Japanese]

Martin, A.M. and S.K. Goffredi. 2011. *'Pliocardia' krylovata*, a new species of vesicomyid clam from cold seeps along the Costa Rica Margin. Journal of the Marine Biological Association of the United Kingdom doi: 10.1017/S0025315411000713: 1–11.

Okutani, T., K. Fujikura, and S. Kojima. 2000. New taxa and review of vesicomyid bivalves collected from the northwest Pacific by deep-sea research systems of Japan Marine Science &Technology Center. Venus, 59: 83–101.

Okutani, T., S. Kojima, and N. Iwasaki. 2002. New and known vesicomyid bivalves recently collected from the western and central Nankai Trough off Shikoku and Honshu, by deep sea research systems of Japan Marine Science and Technology Center. Venus: 61, 129–140.

Olsson, A.A. 1931. Contributions to the Tertiary paleontology of northern Peru: Part 4, The Peruvian Oligocene. Bulletins of American Paleontology 17: 97–264.

Otuka, Y. 1939. Mollusca from the Cainozoic System of eastern Aomori Prefecture, Japan. Journal of the Geological Society of Japan 46: 23–31.

Sasaki, T., T. Okutani, and K. Fujikura. 2005. Molluscs from hydrothermal vents and cold seeps in Japan: A review of taxa recorded in twenty recent years (1984–2004). Venus 64: 87–133.

Sturany, R. 1896. Mollusken I (Prosobranchier und Opisthobranchier; Scaphopoden; Lamellibranchier) gesammelt von S.M. Schiff "Pola" 1890-94. Denkschriften der mathematisch-naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften, Wien 63:1–36.

Taviani, M. 1994. The "calcari a *Lucina*" macrofauna reconsidered: Deep-sea faunal oases from Miocene-age cold vents in the Romagna Apennine, Italy. Geo-Marine Letters, 14: 185–191.

Taylor, J.D. and E.A. Glover. 2010. Chemosymbiotic bivalves. In: S. Kiel (ed), The Vent and Seep Biota. Topics in Geobiology, pp. 107–136. Springer, Heidelberg.

Takeda, H. 1953. The Poronai Formation (Oligocene Tertiary) of Hokkaido and South Sakhalin and its fossil fauna. Studies on Coal Geology, the Hokkaido Association of Coal Mining Technologists 3: 1–103.

Thiele, J. and S. Jaeckel. 1931. Muscheln der Deutschen Tiefsee Expedition. Wissenschaftliche Ergebnisse der Deutschen Tiefsee Expedition 1898–1899 21: 159–268.

Woodring, W.P. 1925. Miocene mollusks from Bowden, Jamaica. Part I: Pelecypods and Scaphopods. Carnegie Institution of Washington, Publication 366: 1–222.

Research Note

Late Pleistocene *Colus stimpsoni* (Mörch, 1868) (Gastropoda: Buccinidae) from a seabed core (2520 m) in the western North Atlantic

We recovered a shell of *Colus stimpsoni* (Mörch, 1868) from a seabed piston core (8.5 cm diameter) taken at a depth of 2520 m, approximately 15 km south of the most seaward extension of Block Canyon, off Long Island, New York, USA (39°28.00′N, 71°03.78′W). The shell (Figure 1) was positioned 4.6 m below the core top (seafloor), and was radiocarbon dated to 51,700 ± 6,500 ybp (Lab ID: OS-83306), during the last glacial advance of the Pleistocene. The biota preserved in cores typically consists of meiofaunal elements, principally foraminiferan tests, and ostracod carapaces. It is rare to find nearly complete shells of larger macrofaunal species like *C. stimpsoni* because low temperatures and high pressures at great depths cause high carbonate dissolution rates. There is very little fossil evidence of any kind for deep-sea macrofaunal taxa.

Colus stimpsoni is a common species in present-day benthic communities of the continental shelf and upper bathyal zone of the western North Atlantic. It ranges from 34.5° to 56° N, from 50° to 75° W, and from 16 to 1103 m in depth (Rosenberg, 2009; and M.G. Harasewych, personal communication). The core specimen is from 1400 m deeper than the modern bathymetric range limit, and is much larger in size than gastropods currently living at 2500 m. The deep sea is an energy-poor environment that selects for small body size in mollusks (McClain et al., 2009). The size of the shell (Figure 1), which is broken, is 95.0 mm (height + width). Based on the shape of intact living shells, we estimate the complete specimen to have measured 136.4 mm (height + width). A statistical analysis of shell size, using quantile regression, performed on an extensive collection of modern deep-sea gastropods (3426 individuals of 83 species) from the western North Atlantic, predicted a maximum size (height + width) of only 28 mm at 2500 m (McClain et al., 2009). A complete specimen of *C. stimpsoni* would be five times this size in terms of linear dimensions, and even larger in terms of biovolume.

It is conceivable that ocean cooling and increased productivity during glaciation (Yasuhara and Cronin, 2008) could have permitted downward range extensions and larger body size in deep-sea macrofaunal species. Bathymetric range shifts during glaciation are known for meiofaunal species (Kurihara and Kennett, 1988; Cronin and Raymo, 1997). Deep-sea ostracods increased in size with global cooling during the Cenozoic (Hunt and Roy, 2006). In modern deep-sea gastropods in the western North Atlantic, body size increases with depth across the bathyal zone to around 3000–4000 m, and then decreases at abyssal depths (McClain et al., 2005). Since productivity in the form of particulate organic carbon flux to the seafloor decreases exponentially with depth (Rex et al., 2006), body size and productivity are inversely correlated in the bathyal zone. This suggests that increased productivity would not favor larger size at this depth, although it is clearly associated with larger size in coastal species. It is difficult to reconstruct paleoenvironments and their effects on the deep-sea macrofauna in a precise way, but a downward range shift of 1400 m and such a huge increase in body size seem remarkable.

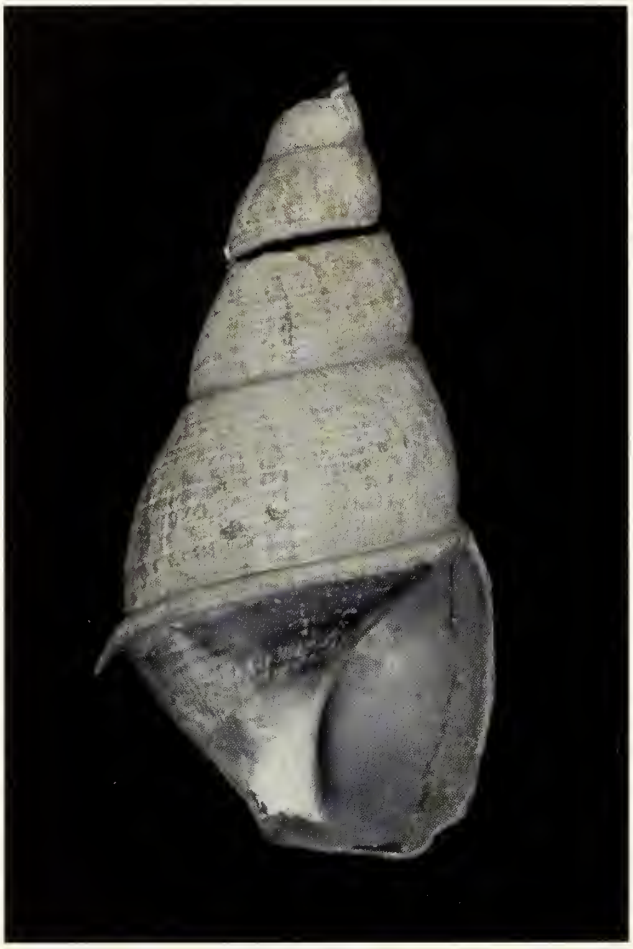

Figure 1. Shell of *Colus stimpsoni* (Mörch, 1868) from a deep seabed core taken at 2520 m south of Long Island, New York, USA (core number OC463-19PC, 39°28.00′ N, 71°03.78′ W, R/V Oceanus Cruise 463, June 19, 2010). The specimen was located 4.6 m below the core top, and was radiocarbon dated to 51,700 ± 6,500 ybp. Shell height 62.8 mm, width 32.2 mm. Catalogue number 374361, Department of Mollusks, Museum of Comparative Zoology, Harvard University. Photograph by Leo Kenney.

The Pleistocene was a period of active canyon formation and large-scale downslope transport of sediment (Emery and Uchupi, 1984). The area where the core was

taken shows evidence of extensive debris flow (O'Leary, 1996; Chaytor et al., 2011). Several mechanisms that could be responsible for the presence of *Colus stimpsoni* in a seabed core at 2520 m are being investigated, including downslope transport as part of a sediment-laden gravity flow and deposition via ice-rafting. While the shell's occurrence in the core is probably a spurious locality record for the range of living populations, it does provide an important temporal reference point. *Colus stimpsoni* was a constituent of Pleistocene communities extending back to at least 45,000 ybp. It survived the last glaciation, which either must have obliterated much of its geographic range through lower sea level and ice cover or shifted it southward, as well as subsequent episodes of abrupt climate change that appear to have caused widespread extinction of the upper bathyal deep-sea fauna (Yasuhara et al., 2008).

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LITERATURE CITED

Chaytor, J.D., U.S. ten Brink, D.C. Twichell, C.D.P. Baxter, T.D. Hallam, and D.S. Brothers. 2011. Submarine landslides along the U.S. Atlantic margin: their distribution, failure processes, and age. American Geophysical Union, Fall Meeting Abstract T21A-2302.

Cronin, T.M. and M.E. Raymo. 1997. Orbital forcing of deep-sea benthic species diversity. Nature 385: 624–627.

Emery, K.O. and E. Uchupi. 1984. The Geology of the Atlantic Ocean. Springer-Verlag, New York, 1050 p. + 23 separate charts.

Hunt, G. and K. Roy. 2006. Climate change, body size evolution, and Cope's rule in deep-sea ostracodes. Proceedings of the National Academy of Sciences, USA 103:1347–1352.

Kurihara, K. and J.P. Kennett. 1988. Bathymetric migration of deep-sea benthic foraminifera in the southwest Pacific during the Neogene. Journal of Foraminiferan Research 18:75–83.

McClain, C.R., M.A. Rex, and R.J. Etter. 2009. Patterns of deep-sea macroecology. In: J.D. Witman and K. Roy (eds.) Marine Macroecology. University of Chicago Press, Chicago, pp. 65–100.

McClain, C.R., M.A. Rex and R. Jabbour. 2005. Deconstructing bathymetric body size patterns in deep-sea gastropods. Marine Ecology Progress Series 297:181–187.

O'Leary, D.W. 1996. The timing and spatial relations of submarine canyon erosion and mass movement on the New England continental slope and rise. In: J.V. Gardner, M.E. Field and D.C. Twichell (eds.), Geology of the United States' Seafloor: The View from GLORIA. Cambridge University Press, New York, pp. 47–58.

Rex, M.A., R.J. Etter, J.S. Morris, J. Crouse, C.R. McClain, N.A. Johnson, C.T. Stuart, J.W. Deming, R. Thies and R. Avery. 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. Marine Ecology Progress Series 317: 1–8.

Rosenberg, G. 2009. Malacolog 4.1.1: A database of western Atlantic marine Mollusca. [WWW database (version 4.1.1)] URL http://www.malacolog.org/.

Yasuhara, M. and T.M. Cronin. 2008. Climatic influences on deep-sea ostracode (Crustacea) diversity for the last three million years. Ecology 89: S53–S65.

Yasuhara, M., T.M. Cronin, P.B. deMenocal, H. Okahashi and B.K. Linsley. 2008. Abrupt climate change and collapse of deep-sea ecosystems. Proceedings of the National Academy of Sciences USA 105: 1556–1560.

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ABSTRACT

The new genus *Xeniostoma*, type species *X. inexpectans* new species, occurs from 200–400 m, off the western Aleutian Islands, Alaska, in association with vase-shaped hexactinellid sponges of the family Rossellidae. The feathery radula of *Xeniostoma* indicates an allocation to the Calliostomatidae. It is assigned to the new subfamily Xeniostomatinae because it lacks the massive inner marginal teeth that function in the carnivorous feeding of other genera in the family. There is no evidence of spongivory; its feathery teeth are suitable for feeding on detritus that accumulates on the host sponge.

Xeniostoma is also unusual in the family Calliostomatidae for its shell with rounded whorls, lack of spiral sculpture, large protoconch, and lack of teleoconch 1, its lack of jaws, and lack of the pseudoproboscis; it is also unusual in having a large right suboptic tentacle. The very large protoconch suggests that only a few large eggs are produced and that larvae can gain protection among the large projecting spicules on the outer surface of the host sponge. Within the Calliostomatidae, *Xeniostoma* most resembles the nearly smooth-shelled Magellanic genera *Photinula* Adams and Adams, 1854 and *Photinastoma* Powell, 1951, which have morphology of the lateral teeth in common and a similar shell profile, but have the other characters expected in carnivorous calliostomatids of the subfamily Calliostomatinae.

The typical subfamily Calliostomatinae exhibits an extreme level of specialization that sets it apart from other trochiform vetigastropods. If other living or fossil genera become known, there would be further support for the hypothesis that Xeniostomatinae could represent a surviving member of a nearly extinct basal group within Calliostomatidae.

One other trochiform vetigastropod family, the smaller-shelled Trochaclididae, is also hosted by deep-water hexactinellid sponges of the family Rosellidae. A reconsideration of the feathery radula of Trochaclididae leads to the conclusion that it too is suitable for detrital feeding.

Additional keywords: Calliostomatidae, Xeniostomatinae, Trochaclididae, Rosellidae, spongivory, Hexactinellid sponges

INTRODUCTION

Benthic sampling for resource-monitoring purposes has been conducted in recent years by the National Marine Fisheries Service in the vicinity of the Aleutian Islands, Alaska. New species of mollusks have been recognized by the late Rae Baxter and by Roger N. Clark; descriptions of further new species will be forthcoming.

Among the new findings is a remarkable new monotypic genus *Xeniostoma* and new species *inexpectans*, for which the smooth shell resembles the trochid genus *Margarites* in the subfamily Margaritinae, and the Magellanic genus *Margarella* in the subfamily Gibbulinae, but radular characters of the new genus are indicative of the family Calliostomatidae. Within the Calliostomatidae, the closest comparison in shell profile is with the Magellanic genera *Photinula* H. and A. Adams, 1854 and *Photinastoma* Powell, 1951, which have nearly smooth shells unlike those of most other calliostomatids. Comparisons are made in the descriptions of the new genus and species to the type species *Photinula coerulescens* (King and Broderip, 1831), from southern Argentina and Chile (Figures 9-11) and *Photinastoma taeniata* (Wood, 1850), from southern Argentina (Figures 12–13).

A number of questions about the affinity and its possible phylogenetic significance are raised by this discovery. The taxonomic question requires resolution by the placement in a new subfamily of Calliostomatidae. Another question of major interest concerns the association of the new species with hexactinellid sponges. This requires comparison with two other groups of trochiform gastropods that have previously been reported to occur on vase-shaped sponges of the family Rosellidae in the sponge order Hexactinellida. No information about this group of sponges has been provided in the accounts of the gastropods; this omission is addressed here with references to the literature on hexactinellid biology.

The best known gastropod family associated with hexactinellid sponges is the small-shelled trochiform vetigastropod family Trochaclididae Thiele, 1928, all members of which are known to be associated with hexactinellid sponges (Marshall, 1995b, and references therein). In previous reports on the Trochaclididae, there has been no information pertaining to the sponges.

Another species of comparable size and morphology identified by Gutt and Schicken (1998) as "*Margarella* sp." [likely *M. antarctica* Lamy, 1905], is also associated with hexactinellid sponges of the family Rosellidae in the Antarctic fauna. The genus *Margarella* Thiele, 1893, has most recently been assigned to the subfamily Gibbulinae of the Trochidae by Zelaya (2004).

The new calliostomatid genus *Xeniostoma* represents the third known vetigastropod group known to be associated with vase-shaped sponges of the order Hexactinellida.

Questions about the association of these gastropod families with the hexactinellid sponges are raised: Are these gastropods feeding directly on the sponges or are they feeding on detritus that accumulates on the sponges? What other benefits are derived from the association of these gastropods with the sponges?

MATERIALS AND METHODS

The new species has come to light due to collecting efforts of the late Rae Baxter and subsequently by Roger N. Clark, both of whom have obtained specimens in the process of salvaging invertebrate specimens from the trawl catches, while aboard survey vessels during summer cruises at the Aleutian Islands.

Specimens were preserved directly in ethyl alcohol of unknown strength, without relaxation or fixation. The preservation of all material for the new species is not adequate for thorough analysis. Preserved bodies of the specimens have been twisted out of the shell, but bodies of all specimens are torn, with the visceral mass not remaining attached to the head-foot. The head-foot material is suitable for study of the external anatomy and the radula; the macerated remains of the viscera are suitable for examination of gut contents, but not for determining the condition of the gonads.

Although none of the records of associated vetigastropods are accompanied by identified sponges, some information on the biology of the hexactinellid sponges is provided here. All three records (*Xeniostoma*, one species of *Margarella*, and all Trochaclididae) mention vase-shaped sponges, which are here noted to be members of the family Rossellidae. A substantial number of genera are known in the Rosellidae, based on the morphology of the siliceous spicules and the size and general morphology of the sponge (see Leys, et al. [1998], and Leys, et al. [2007] for general review of hexactinellid biology).

Abbreviations: F/V, Commercial fishing vessel contracted for survey cruises, by National Marine Fisheries Service; LACM, Natural History Museum of Los Angeles County; USNM, United States National Museum of Natural History, Washington; SEM, Scanning electron microscopy.

SYSTEMATICS

Superorder Vetigastropoda Salvini-Plawen, 1980
Superfamily Troehoidea Rafinesque, 1815

Family Calliostomatidae Thiele, 1924

Remarks: Hickman and McLean (1990) and Hickman (1996) previously treated the group Calliostomatinae as a subfamily of Trochidae, but other recent authors including Marshall (1995a), Warén and Bouchet *in* Bouchet and Rocroi (2005), Williams et al. (2010), have treated this as a full family, as done so here. The most current and comprehensive taxonomic treatment is that of Marshall (1995a), who provided a complete list of generic level taxa of Calliostomatidae. Marshall distinguished two subfamilies in which the sculpture consists of beaded spiral cords, typical Calliostomatinae and Thysanodontinae Marshall, 1985, members of which have a completely different radula of slender teeth with backward directed barbs. Thysanodontinae are not further mentioned here. A third subfamily Xeniostomatinae is proposed here.

Subfamily Calliostomatinae Thiele, 1924

Diagnosis: Spiral sculpture of raised cords, usually strongly beaded; protoconch diameter usually relatively small (diameter 320–420 µm); protoconch with raised hexagonal pattern and apertural rim; short teleoconch I of first quarter whorl; pseudoproboscis well developed; jaws well-developed; inner marginal teeth of radula enlarged.

Remarks: The typical subfamily was further divided into two tribes by Marshall (1995a), the typical Calliostomatini and Fautricini Marshall, 1995, the latter with shell characters not unlike Calliostomatini, but considered by Marshall to exhibit a basal, plesiomorphic condition of the radula for the family.

Subfamily Xeniostomatinae new subfamily

Diagnosis: Profile low, spiral sculpture lacking at all growth stages; protoconch smooth, very large (900 µm); teleoconch I lacking; pseudoproboscis lacking; jaws lacking; inner marginals not enlarged.

Included Genera: Monotypic for *Xeniostoma*, new genus. Other species or genera may await discovery.

Remarks: The lack of enlarged inner marginal teeth distinguish this subfamily from typical members of the subfamily Calliostomatinae. The lack of any spiral sculpture, the lack of jaws, and the lack of the pseudoproboscis are further differences from Calliostomatinae.

Xeniostoma new genus

Type Speeies: *Xeniostoma inexpectans* new species, by original designation.

Deseription: Generic level description as in species description below.

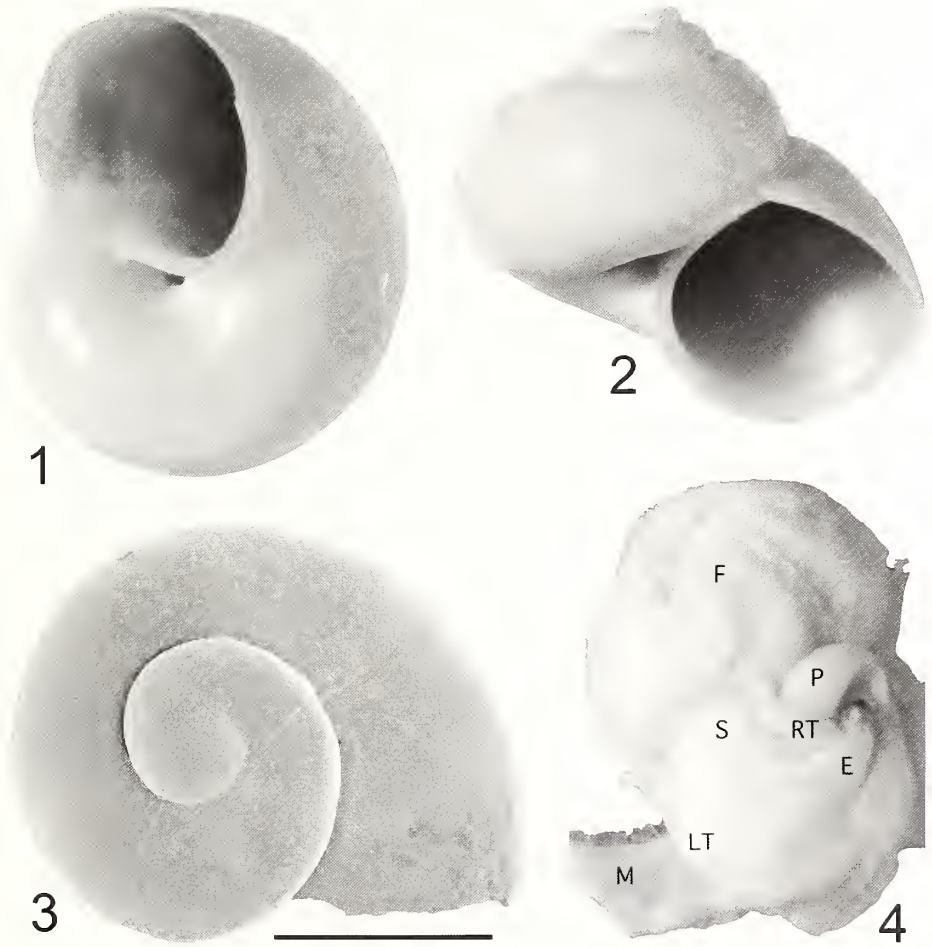
Remarks: The genus is monotypic; once additional species become known, the limits of the genus will be better understood; differences in size at maturity, shell proportions, and shell sculpture can be expected.

***Xeniostoma inexpectans* new species**

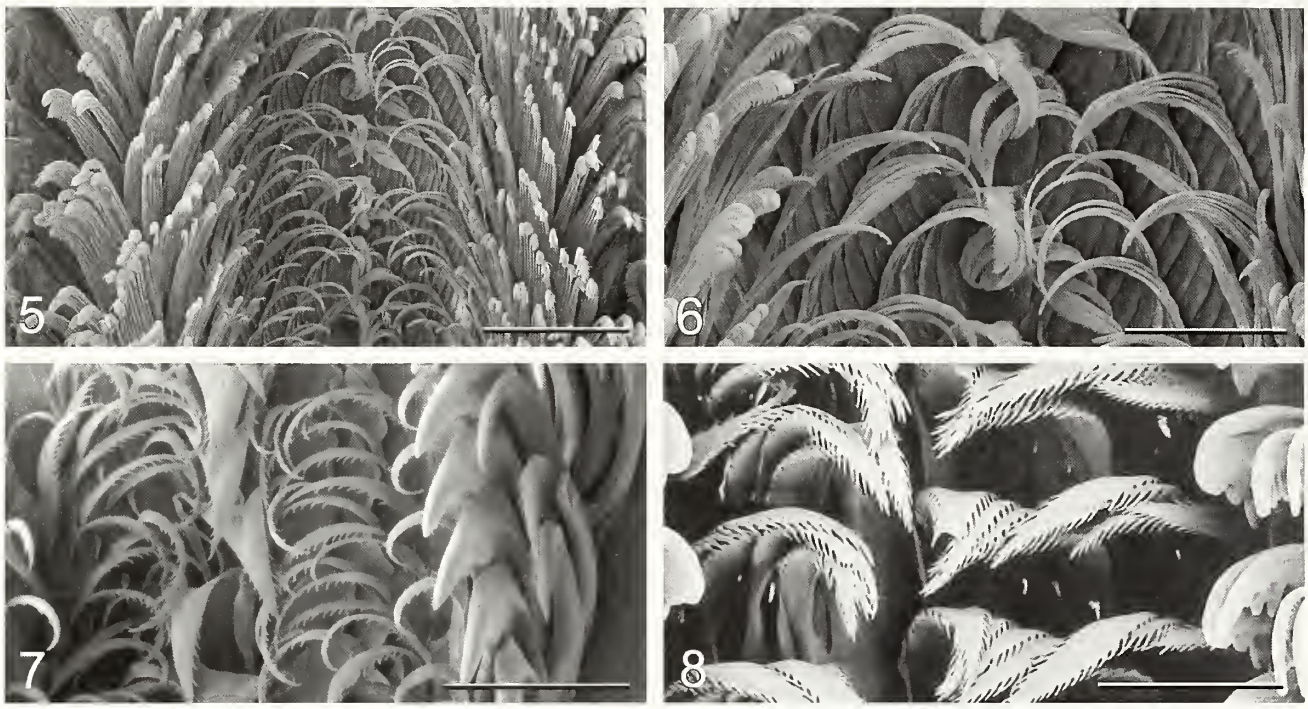
Description: Shell (Figures 1–3): Color silvery white, periostracum fully intact, shiny, thin, tightly adhering; nacre of shell interior strongly iridescent. Shell diameter about 10 mm, whorls 2.7. Whorls rounded but slightly subangulate on shoulder, suture moderately impressed. Surfaee smooth, axial and spiral sculpture lacking, peristome nearly complete. Aperture large, height of aperture more than half height of shell. Umbilicus narrow, umbilical wall rounded. Height 8.7 mm, diameter 9.4 mm (holotype). Protoconch (Figure 3) smooth, bulbous, about 900 µm in maximum diameter, lip not thickened, transition from protoconch to teleoconch weakly indicated. Opereulum corneous, multispiral, about 7 evenly expanding volutions, growing edge fitting the parietal area of the aperture.

External Anatomy (Figure 4): Head/foot with evenly tapered suboptic tentacle below right cephalic tentacle and anterior to short eyestalk, contracted length equivalent to that of cephalic tentacle, diameter twice that of cephalic tentacles, not with apparent fold or groove. Tentacle tip tapered. Cephalic lappets lacking, neck lobes of simple narrow flaps. Eyes large, on short stalks, darkly pigmented. Oral disk lacking pseudoproboscis. Anteriormost pair of epipodial tentacles the largest, more posterior pairs small (contracted in preserved specimens). Jaws not detected. Ctenidium bipectinate, free tip short. Osphradium with simple lamellae.

Radula (Figures 5–6): Central field broad, with about 20 pairs of laterals, with inverted-V alignment of tooth rows. Rachidian tooth with tapered tip and broad base. Lateral teeth with broad bases to shafts, tips long and narrow, extending toward rachidian tooth nearly across central field, with deeply serrated edges away from distal end. Extended tips emerging from inner side of tooth base. Basal part of tooth at least four times broader than emerging tip. Lateral edges of tooth bases thin and



Figures 1–4. *Xeniostoma inexpectans* new genus, new speeies. **1–2.** Holotype, off Kiska Island, Rat Islands, Aleutian Islands, Alaska, 272 m depth, maximum diameter of shell 10.0 mm. **1.** Basal view. **2.** Apertural view **3.** Apical view of immature paratype, showing protoconch and first teleoconeh whorl. Seale bar = 1 mm. **4.** Dorsal view of preserved head-foot of holotype, mantle skirt with gill attached (not showing) folded over to left. Abbreviations: LT, left cephalic tentacle; E, eye stalk; F, foot; M, mantle skirt; SO, right suboptic tentacle; RT, right cephalic tentaele; S, snout. Scale bar = 1 mm.



Figures 5–8. Radulae. **5–6.** *Xeniostoma inexpectans* new genus, new species. **5.** Full width of radular ribbon, showing rachidian tooth at center, approximately 20 pairs of curved lateral teeth with broad bases, and numerous, closely adjacent, relatively straight marginal teeth. Scale bar = 200 µm. **6.** Enlarged view of rachidian and adjacent lateral teeth, showing that the rachidian tooth is only slightly broader than adjacent lateral teeth. Scale bar = 100 µm. **7.** *Photinula coerulescens* (King and Broderip, 1831), partial view of ribbon with 4 complete rows of teeth, at center left showing elongate rachidian teeth with long tapering cusps, flanked by four pairs of lateral teeth on left and right; on right showing large inner marginal teeth, and smaller outer marginal teeth (outmost marginals had been stripped away). Scale bar = 200 µm. **8.** *Photinastoma taeniata* (Wood, 1850), central field of radula, showing rachidian and 6 pairs of lateral teeth; on left and right showing enlarged inner marginal teeth and on right showing adjacent lateral teeth. Scale bar = 100 µm. [SEMs, 5–6, D. Geiger, 7. C. Hickman; 8, A. Warén].

flap-like, lacking interlock, concealing inner edge of adjacent lateral teeth. Marginal teeth numerous, with long shafts and much shorter denticle bearing tips. Inner marginal teeth with short denticles, size of inner marginal teeth not larger than other marginal teeth.

Holotype: LACM 2971 (ex LACM 97-162)

Type Locality: 272 m, W of Kiska Island, Rat Islands, Aleutian Islands, Alaska (51°54.31′ N, 176°35.89′ E), F/V Dominator (sta. 23-971-202), R. N. Clark, 1 August 1997. One live-collected specimen (Figure 1).

Paratypes: LACM 2972 (ex LACM 86-330), 219 m, NE of Semisopochnoi Island, Rat Islands, Aleutian Islands (52°24.09′ N, 179°42.84′ E), Rae Baxter, 10 September 1986; one live-collected specimen and two smaller, dead specimens; maximum diameter 4.8 mm (used for initial radular preparation); one small shell coated for SEM of protoconch (Figure 3); LACM 2973 (ex LACM 97–168), 325 m, SW of Buldir Island, Aleutian Islands (52°18.50′ N, 175°49.0′ E), F/V Dominator (sta. 23-971-243), R. N. Clark, 9 August 1997; 3 specimens, 2 live-collected.

LACM 2974 (LACM 97-156), 384 m, SW of Amchitka Island, Rat Islands, Aleutian Islands, Alaska (51° 27.70′ N, 178° 35.0′ E), F/V Dominator (sta. 23-971-181), R. N. Clark, 27 July 1997. 2 live-collected specimens; LACM 3233, 221 m, NW of Kiska Island, Rat Islands, Aleutian Islands, Alaska (52°9.58′ N, 175°11.67′ E), F/V Gladiator (sta. 147-04-195), R. N. Clark, 25 July 2004. 7 large specimens (1of 3 LACM specimen used for radular SEM, figures 5–6); one paratype, USNM 1184071, and 3 paratypes R. N. Clark Collection.

Distribution and Depth: Rat Islands, western Aleutian Islands, Alaska, from Buldir Island toward the west, to Semisopochnoi Island toward the east, from moderately deep water, depths ranging from 219–384 m. An association of the new species with vase-shaped hexactinellid sponges of the family Rosellidae has been confirmed, based on the eight additional specimens collected with the sponge from Kiska Island, Aleutian Islands, during the summer of 2004 by Roger Clark.

Etymology: The prefix *xeno* is Greek, *xenos*, a stranger, suggested by the strange combination of characters in the new genus. The root *-iostoma* is based on *Calliostoma*,

the nominate genus of the typical subfamily. The specific name means unexpected.

Comparative Remarks: Shell. The smooth shell resembles that of the trochid subfamily Margaritinae, particularly the Aleutian Island species *Margarites hickmanae* McLean, 1984, in its large size and silvery white coloration, but differs in its complete lack of spiral sculpture and its larger protoconch size. See McLean (1984) for illustration of *M. hickmanae*.

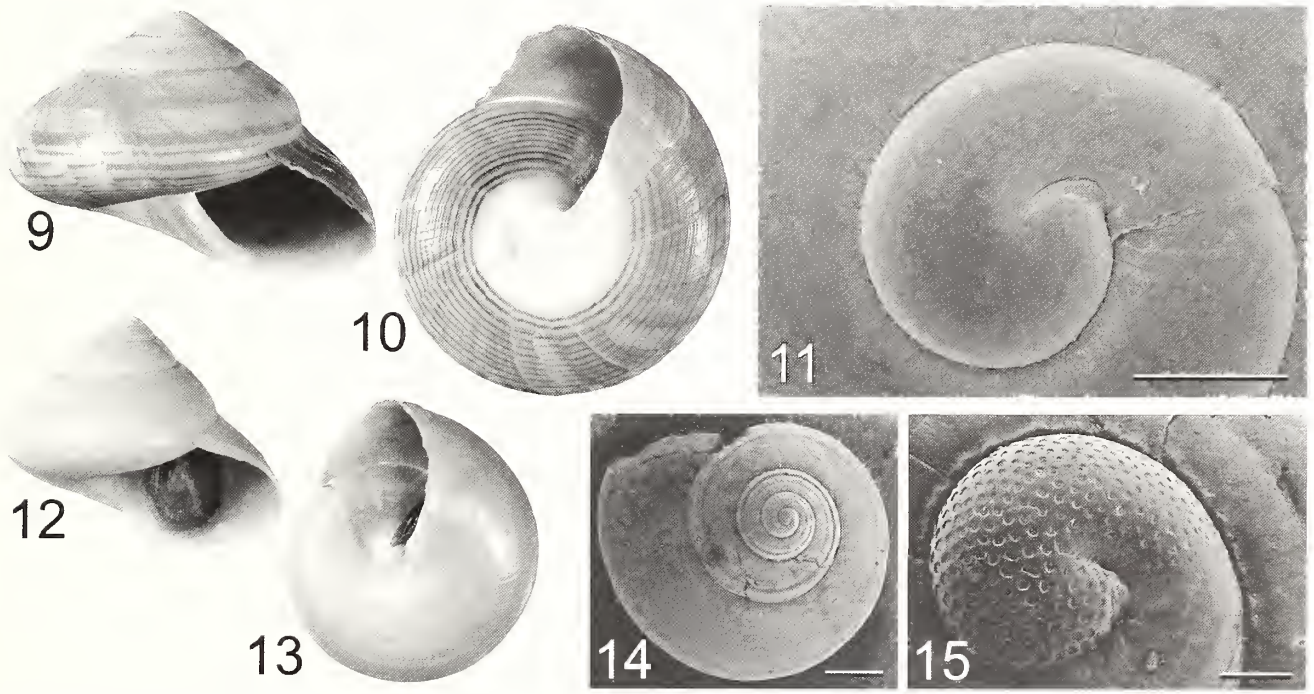
The smooth shell is unusual for Calliostomatidae; most species of *Calliostoma* and related genera have a high shell profile, often with flat sides. The sculptures of typical species consist of complexly beaded spiral cords. Among the Calliostomatidae, the rounded whorls and the smooth shell of *Xeniostoma* are comparable to the genera *Photinula* (Figures 9–11), which has faint spiral sculpture, and to *Photinastoma* (Figures 12–15), which has more strongly indicated spiral cords in the early teleoconch (Figure 14, 15).

Protoconch. The protoconch at a diameter of 900 µm lacks the typical hexagonal micro-sculpture of most calliostomatids (see Hickman and McLean, 1990, fig. 70D), and is larger than that known for most trochoideans, in which the usual protoconch diameter is about 200–300 µm (Hickman and McLean, 1990). Loss of the hexagonal sculpture would be expected with size increase of the protoconch. The protoconch of *Photinula coerulescens* is shown here for comparison (Figure 9). It has a diameter of about 500 µm, lacks the hexagonal sculpture and lacks the inflated lip edge. The protoconch of *Photinastoma* is also large, but has broad pits that diminish in size near the edge.

Teleoconch I. Marshall (1995: 385, figs. 2–3) indicated that typical calliostomatines have a short segment known as teleoconch I, followed by a growth scar on the first quarter teleoconch whorl, which marks a change to the mature sculpture. This is lacking altogether in *Xeniostoma* (Figure 3), but very faintly indicated in *Photinula coerulescens* (Figure 9), and in *Photinastoma taeniata* (Figure 15).

Radula. The radula of *Xeniostoma* (Figures 5, 6) has the rachidian and lateral teeth with a long, narrowly constricted upper region of the shaft, with deep serration on the edges, having a strong resemblance to the outer lateral teeth of the calliostomatid genus *Photinula* (Figure 7) and *Photinastoma* (Figure 8), but having a much narrower rachidian tooth and not the enlarged inner marginals. The inner marginal teeth of *Xeniostoma* have the appearance of calliostomatid marginal teeth at the outer zone, but these inner marginal teeth are not enlarged, as in *Photinula* and *Photinastoma*, and all other calliostomatid radulae.

Jaw Plates. Jaw plates in calliostomatids are large, dark brown, and readily observed in preserved specimens through a dorsal cut made on the snout between



Figures 9–15. Shells and early whorls of *Photinula* and *Photinastoma*. **9–11.** *Photinula coerulescens* (King and Broderip, 1831). **9–10.** Mature shell (LACM 54671), intertidal, Posesion, Chile, height 20.0, diameter 27.9 mm. **9.** Apertural view. **10.** Basal view. **11.** SEM view of apex of small specimen, showing smooth protoconch with pinched tip and lacking apertural rim (LACM 71-30), 75 m, SE of Tierra del Fuego, Chile. Scale bar = 200 µm. **12–15.** *Photinastoma taeniata* (Wood, 1850), Mature shell (LACM 29116), Punta Foca, Puerto Deseado, Argentina, height 9.3, diameter 11.6 mm. **12.** Apertural view. **13.** Basal view. **14–15.** SEM views of apical whorl and protoconch. **14.** Apical whorl. Scale bar 1 mm. **15.** Protoconch. Scale bar = 100 µm. [14–15, SEM by A. Warén].

the cephalic tentacles (see Hickman and McLean, 1990, fig. 68G). No jaws were found for *Xeniostoma*, but the jaws of *Photinula* are large, as in other calliostomatids.

Pseudoproboscis. *Xeniostoma* lacks the calliostomatid pseudoproboscis; a pseudoproboscis is present in *Photinula*. The pseudoproboscis of calliostomatids is a shallow groove on the oral disk (see Hickman and McLean, 1990: fig. 70B).

Suboptic tentacle. *Xeniostoma* is the first known calliostomatid genus to have a large right suboptic tentacle in mature specimens, as shown in Figure 4. All specimens examined have this structure. This might be construed as a cephalic penis (see Kano, 2008), but it is found on all specimens, which would additionally require the assumption that the species is hermaphroditic. The sex is not known for any of the specimens. The material is not sufficiently well preserved for me to establish a function for the structure, and to establish that the gonad is hermaphroditic. The most likely interpretation (A. Warén, pers. comm.) is that it represents a hyper-development of the anterior right "lateral appendage," of the calliostomatid larval stage, as illustrated by Ramon (1990: fig. 3).

DISCUSSION

Association of Trochiform Vetigastropods with Hexactinellid Sponges: Specimens of *Xeniostoma*, the trochid *Margarella antaretica* (as reported by Gutt and Schicken, 1998), and all species in the family Trochaclididae are associated with glass sponges of the Class Hexactinellida, family Rosellidae (the deep-water vase sponges). The association of *Margarella* and the Trochaclididae are further discussed below.

The most recent general summary of hexactinellid biology is that of Leys et al. (2007). One species of rosellid sponge, *Rhabdoealyptus dawsoni* (Lambe 1892), has been well studied because it accessible to divers off southern Vancouver Island, British Columbia. Studies on the biology of this species are those of Boyd (1981), and Leys and Lauzon (1998), with further details provided by Leys et al. (2007). This species lives at depths below 20 m on the walls of fjords and sloping bottoms below walls of the fjords. Long spicules project beyond the outer wall of *Rhabdoealyptus*, forming a dense veil of spicules that harbors a microfauna of invertebrates (Boyd, 1981), including small crustaceans, polychaetes, small bivalves, and cerithiopsid gastropods, all of which live within the spicule veil for protection from predators and benefit from the flow of particles produced by the pumping action of the sponge. The veil may become clogged with detritus, but the sponge is capable of sloughing off the outer layers of the mat, which is usually accomplished in the winter months.

Another northeastern Pacific genus is *Staurocalyptus*, which produces long spicules that project straight out from the body of the sponge (see *S. solidus* Shulze, 1889, as shown on the cover illustration of Green and Bakus, 1994); the long spicules of this genus also produce a microhabitat that provides protections for small invertebrates. According to Reiswig (pers. comm.), the large atrial cavities of rosellid sponges are kept free of sediment by the force of the out-current flow generated by the sponge; these cavities are utilized by larger invertebrates and fishes, and are thus not suitable as a refuge for small gastropods.

Small-shelled vetigastropods of the families Calliostomatidae (*Xeniostoma*), Trochidae (*Margarella*), and Trochaclididae (*Troehaelis*) would be able to find protection from predators within the outer veil of rosellid sponges and would be provided with a continuous flow of detritus. Species in each of these genera are equipped with smooth shells devoid of projecting sculpture, which would enable navigation through a veil or thicket of long, external spicules.

Modifications of the Calliostomatid Radula and Feeding in *Xeniostoma*: Marshall (1995: 386) noted: "As shown by Warén (1990), the calliostomatine radula is distinctive among trochoideans in that the innermost pair of marginals become greatly enlarged at an extremely early stage of ontogenesis, after which the central and lateral teeth arise by intercalation in the central field." The large inner marginal teeth of calliostomatids are also illustrated by Hickman and McLean (1990, figs. 71A, E). It is these enlarged marginal teeth that are the working teeth of calliostomatids, whether feeding on cnidarians or demosponges. Sponge feeding in the non-silicate Demospongia has been infrequently reported in Calliostomatidae (see Marshall, 1988: 228), but there is no previous mention of any member of Calliostomatidae feeding on hexactinellid sponges.

The fact that the innermost marginal teeth of *Xeniostoma* are not enlarged at any stage is a clear indication that this is a radula otherwise unknown in the Calliostomatidae. This indicates that *Xeniostoma* is not carnivorous, as expected in all other calliostomatids. It seems most reasonable that, because *Xeniostoma* does not have any teeth in the radula that are robust enough to function in sponge feeding, the only other option left for such a feathery radula is to assist in feeding on detrital particles, available within the veil of long spicules that project away from the body of the rosellid sponge. There is a source of detritus that settles on hard bottoms in sublittoral zones, in addition to pumping activity of the sponge that would provide a source of detritus flowing toward the outer body wall of the sponge.

Marshall (1995a) considered detritivory to be the mode of feeding in the post-veliger larval stages of calliostomatids. With regard to the termination of the teleoconch I stage at the end of the first quarter of teleoconch growth, Marshall (1995: 385) stated: "It seems clear that the post-larval scar represents a growth pause of a crisis period and I suggest that it may denote the transition to exclusive detritivory (later transitional to carnivory). It may actually mark the transition to carnivory in some species, though the radula may be insufficient to deal with Cnidaria or sponges at such an early stage of development. This interpretation differs from that of

Hickman (1992, fig. 5G), who identified the terminal protoconeh varix and the varix following it as denoting the times of hateling and settlement respectively."

Retention of this mode of feeding at maturity is therefore a simple hypothesis for the feeding of *Xeniostoma*. This is confirmed by my finding no sponge spicules in the maeerated viseeral residue of any examined speeimens of *Xeniostoma*.

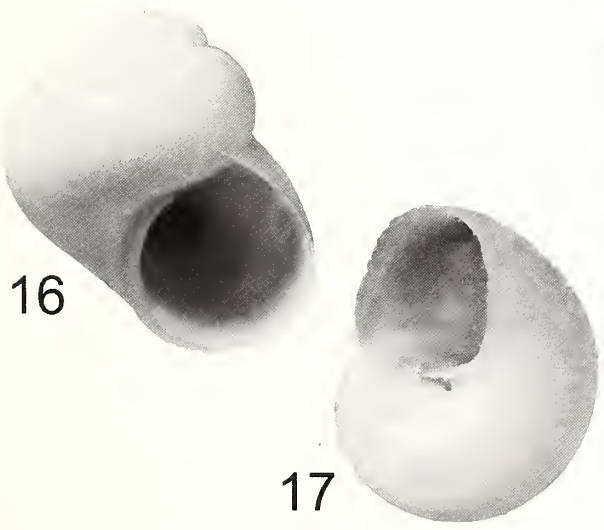
Egg Size and Protoconch Size in *Xeniostoma*: Males of most species of Calliostomatidae broadeast their gametes, whieh stimulates females to produce eggs, which are laid in gelatinous strings, with fertilization taking plaee externally (e.g., Ramon, 1990: 322). Larvae of many speeies hateh and exit the egg strings as post-torsional veligers (Hickman, 1992). The unusually large protoconeh of *Xeniostoma* is indicative of direct development from large, yolky eggs. Relatively few eggs eapable of forming a protoconch at such a large diameter of 900 microns eould be produced. The veil of spicules on the outer wall of the sponge would provide an ideal site for the early stages of growth in *Xeniostoma*, in affording protection as well as a steady source of detritus.

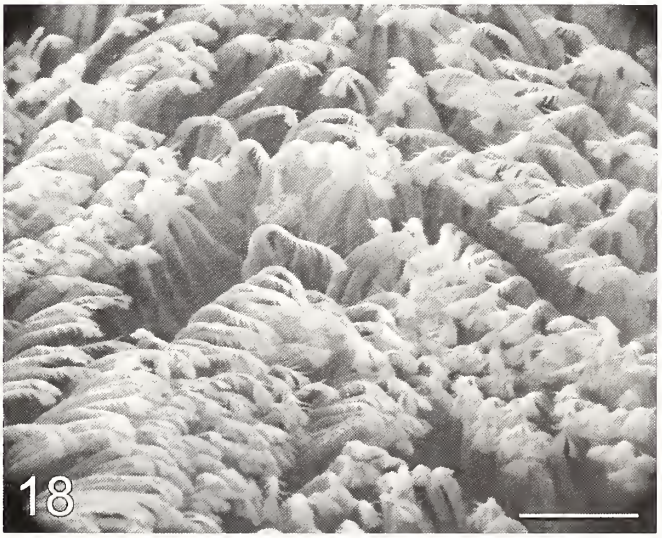
Loss of the usual micro-seulpture of ealliostomatid protoconehs is a function of increased size. Large protoeonchs are indicative of large egg size, direct development, and redueed dispersal eapabilities. Other large protoconehs lacking the typical hexagonal microsculpture are known in Calliostomatidae; in the deep-sea speeies *Falsimargarita nanduri* Warén and Bouchet 2001 the 1.2 mm diameter protoconch is smooth (Warén and Bouehet, 2001: 133, fig. 8e).

Feeding in *Margarella Antarctica*: Gutt and Schickan (1998: 403) stated that the Antarctic speeies "*Margarella* sp. 1" oeeurs on the glass sponges of the *Rosella/Scolymastra* group, and that "*Margarella* sp. 1 cleans but also feeds on the sponges, thus having both a positive and negative effect on the host." I have not found a detailed account of this relationship in papers cited therein, but the radula of all speeies of *Margarella* has the rachidian and the lateral teeth with strong cusps (see Zelaya, 2004), so it is conceivable that the teeth of the central field would be eapable of feeding directly on the tissue of the hexactinellid sponge, and the marginal teeth would also clean the detritus that aecumulates on the sponge.

Feeding in Trochaclididae: The radula of *Acremodonta*, a genus now assigned to the Trochaclididae, was illustrated by Marshall (1983); that of *Trochaclis* was first illustrated with SEM by Warén (1989). These genera have finely divided tips to the numerous teeth, in which the rachidian, laterals and marginals are of similar morphology. The shell of *Trochaclis* species (Figures 17, 10), is much smaller and of higher profile than that of *Xeniostoma*. Here I illustrate the radula (Figure 18) of a yet undescribed speeies of *Trochaclis*, which shows fully extended lateral teeth with feathery tips. This was prepared by critical point drying of the whole radular ribbon, which provides an improvement over that of most illustrations of the radula of *Trochaclis*, in which the most terminal divisions of the eusps are often clumped together.

All records of troehaclidids indicate an association with hexactinellid, vase-shaped sponges (see Marshall, 1995a), although none of the sponges have been identified in previous accounts. In a review of the speeies of the southwestern Pacific in the vicinity of New Zealand, Marshall (1995a) stated for the family that "gut contents indicate spongivory." In an effort to confirm this assumption, I examined the macerated viscera of an unnamed species of *Trochaclis* colleeted from a vase sponge from deep water in the Gulf of Alaska by the late Rae Baxter.





Figures 16–18. Family Trochaclididae, shell and radula of undescribed species of *Trochaclis* from Gulf of Alaska. **16–17.** Shell, height 3.9 mm. **18.** Critical-point dried radula. Scale bar = 20 μm.

I found only a few of the smaller spicules that comprise the body in a rosellid sponge, rather than finding the gut to be paeked with sponge spieules. There should be a few spieules that would be shed by the sponge if *Trochaclis* is feeding on detritus, for which its radula is suited. I therefore eonelude that *Trochaclis* is also a detrital feeder.

Implications for the Evolution and Higher Classification of Calliostomatidae: Two genera from southern South Ameriea, *Photinnla* and *Photinastoma*, laek the strongly beaded sculpture of typieal ealliostomatids, but have other features of typical calliostomatids, ineluding jaws and the pseudoproboscis. Their protoconchs are relatively large; that of *Photinula* (Figure 11) is smooth and that of *Photinastoma* (Figure 15) has pits that suggest a eondition eomparable to the hexagonal structure of typical calliostomatids with smaller protoconehs. There is early spiral sculpture in the teleoeonch of *Photinastoma* (Figure 14). These two genera are therefore retained in the subfamily Calliostomatinae.

Charaeters of the shell, anatomy, and radula of *Calliostoma* and related genera are sufficiently unlike those of all other trochoideans to justify the family level status currently accepted for Calliostomatidae. On the shell alone, the species of *Calliostoma* in its familiar sense are unlike all other trochoideans in their intrieately beaded seulpture and in having the short phase of teleoconch I, representing a suite of charaeters by which the shell, whether living or fossil, may readily be distinguished from all other trochoideans. These features are so elaborate that they are unlikely to be basal in the family and would have been derived from something mueh simpler in shell sculpture (Marshall, pers. comm.).

The nearly smooth shell of *Xeniostoma* may well represent a remnant of the basal or stem eondition for the family, with shells so unremarkable that there may be a hidden fossil reeord with unreeognized roots that are deep in geologie time. I am therefore proposing a new subfamily Xeniostomatinae, whieh eould prove to be the basal subfamily for Calliostomatidae, if other genera for living or extinct speeies are recognized in the future. The other possibility is that all the derived eharacter states of Calliostomatidae have been lost in *Xeniostoma*.

It may be possible to get useful information from moleeular sequence information from *Xeniostoma*. If it fits near other species, it is probably a loss of derived charaeters. If it stands apart, there would be evidence for a deeper division in the family.

ACKNOWLEDGMENTS

I am grateful to the late Rae Baxter, who first eollected the new species, and to Roger Clark for subsequent material of *Xeniostoma inexpectans*. Daniel L. Geiger (Santa Barbara Museum of Natural History) provided SEM images of the radula of a mature speeimen. Carole Hickman (University of Califonia, Berkeley), generously provided the SEM image of a previously prepared radula of *Photinnla coerulescens*. Anders Warén (Swedish Museum of Natural History) furnished images of the early whorls of *Photinastoma taeniata*. Michelle Schwengel (Figures 1–4) and Brian Koehler (Figures 5–10) assisted in the imaging tasks in the preparation of the illustrations. For enlightenment about hexactinellid biology and references to the current literature I thank Henry Reiswig (University of Vietoria, British Columbia). I thank Bruee Marshall (National Museum of New Zealand), for helpful suggestions and for sharing his views about the unknown stem group for Calliostomatidae. I thank Daniel L. Geiger, Ángel Valdés (formerly of LACM), and Anders Warén (Swedish Museum of Natural History, Stoekholm) for helpful suggestions, and Carole Hickman and Bruce Marshall, for thorough reviews of eurrent and previous versions of the manuscript.

LITERATURE CITED

Bouchet, P. and J-P. Rocroi. 2005. Classification and nomenclator of gastropod families. Part 1. Nomenclator of Family-Group Names (Bouchet and Rocroi). Part 2. Working Classification of the Gastropoda (modern "archaeogastropods" by Warén and Bouchet). Malacologia 47: 1–397.

Boyd, I. 1981. The spicule jungle of *Rhabdocalyptus dawsoni*: a unique microhabitat. Unpublished senior honors thesis, University of Victoria, Vancouver, 34 pp.

Green, K.D. and G.J. Bakus. 1994. Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel, edited by J.A. Blake, A.L. Lissner, and P.H. Scott. Vol. 2, The Porifera, 82 pp.

Gutt, J. and T. Schickan. 1998. Epibiotic relationships in the Antarctic benthos. Antarctic Science 10: 398–405.

Hickman, C.S. 1992. Reproduction and development of trochacean gastropods. The Veliger 35: 245–272.

Hickman, C.S. 1996. Phylogeny and patterns of evolutionary radiation in trochoidean gastropods. In: J.D. Taylor (ed.) Origin and Evolutionary Radiation of the Mollusca. Oxford University Press, pp. 177–198.

Hickman, C.S. and J.H. McLean. 1990. Systematic revision and suprageneric classification of trochacean gastropods. Natural History Museum of Los Angeles County, Science Series, no. 35, 169 pp.

Kano, Y. 2008. Vetigastropod phylogeny and a new concept of Seguenzioidea: independent evolution of copulatory organs in the deep-sea habitats. Zoologica Scripta 27: 1–21.

Leys, S.P. and N.R.J. Lauzon. 1998. Hexactinellid sponge ecology: growth rates and seasonality in deep-water sponges. Journal of Experimental Marine Biology and Ecology 230: 111–129.

Leys, S.P., G.O. Mackie, and H.M. Reiswig. 2007. The biology of glass sponges. Advances in Marine Biology 52: 1–145.

Marshall, B.A. 1983. Acremodontinae: a new subfamily of the Trochidae (Mollusca: Gastropoda). Records of the National Museum of New Zealand 2(10): 127–130.

Marshall, B.A. 1988. Thysanodontinae: A new subfamily of the Trochidae (Gastropoda). Journal of Molluscan Studies 54: 215–229.

Marshall, B.A. 1995a. Calliostomatidae (Gastropoda: Trochoidea) from New Caledonia, the Loyalty Islands, and the northern Lord Howe Rise. Résultats des Campagnes Musorstom, 14, Mémoires de la Museum National d'Histoire, Naturelle, Paris (A): 381–458.

Marshall, B.A. 1995b. Recent and Tertiary Trochaclididae from the southwest Pacific (Mollusca: Gastropoda: Trochoidea). The Veliger 38: 92–115.

McLean, J.H. 1984. New species of northeast Pacific archaeogastropods. The Veliger 26: 233–239.

Powell, A.W.B. 1951. Antarctic and sub-Antarctic Mollusca: Pelecypoda and Gastropoda. Discovery Reports 36: 47–196, pls. 1–10.

Ramón, M. 1990. Spawning and development of *Calliostoma granulatum* in the Mediterranean Sea. Journal of the Marine Biological Association, United Kingdom 60: 321–325.

Warén, A. 1989. New and little known Mollusca from Iceland. Sarsia 74: 1–28.

Warén, A. 1990. Ontogenetic changes in the trochoidean (Archaeogastropoda) radula, with some phylogenetic interpretations. Zoologica Scripta 19: 179–187.

Warén, A. and P. Bouchet. 2001. Gastropoda and Monoplacophora from hydrothermal vents and seeps, new taxa and records. The Veliger 44: 116–231.

Williams, S.T., K.M. Donald, H.G. Spencer, and T. Nakano. 2010. Molecular systematic of the marine gastropod families Trochidae and Calliostomatidae (Mollusca: Superfamily Trochoidea). Molecular Phylogenetics and Evolution 54: 783–809.

Zelaya, D.G. 2004. The genus *Margarella* Thiele, 1893 (Gastropoda: Trochidae) in the southwestern Atlantic Ocean. The Nautilus 118: 112–120.

A new species of *Felimare* (formerly *Mexichromis*) (Gastropoda: Opisthobranchia: Chromodorididae) from the Yucatan Peninsula, Mexico

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ABSTRACT

A new species of chromodorid nudibranch from the western Atlantic is described based on three specimens collected in the Campeche Bank, Gulf of Mexico. This new species is assigned to *Felimare*, an allocation based on a new classification of the Chromodorididae established with molecular data. The anatomy and molecular data for this new species are compared to those of other Atlantic species previously assigned to *Mexichromis* (now part of *Felimare*). The new species is characterized by having a primarily white dorsum with two longitudinal blue lines, as well as a yellow band surrounding the mantle margin. Mitochondrial 16S gene data confirms that the new species is genetically different from other Atlantic species of *Felimare* for which molecular data is available.

Additional keywords: Nudibranchia, Gulf of Mexico, 16S mtDNA, anatomy

INTRODUCTION

Rudman (1984) defined *Mexichromis* Bertsch, 1977 (type species *Chromodoris antonii* Bertsch, 1976), as well as other genera of Chromodorididae, based on several anatomical characteristics, primarily the morphology of the mantle glands, oral tube, jaw rodlets, radular teeth, and reproductive system. According to Rudman (1984), *Mexichromis* includes species with mantle glands open ventrally and restricted to a few large glands posteriorly and a few smaller ones along each side; oral tube at least four times the length of the buccal bulb and at least twice the diameter; jaw rodlets ranging from bicuspid to multicuspid; radular teeth bicuspid and denticulate, the denticles being as large or nearly as large as the cusps; reproductive system with a large ramifying vestibular gland covering the ventral surface of the female gland mass and a large exogenous sperm sac (bursa copulatrix) lying down the wide muscular vagina. Although *Mexichromis* initially included only eastern Pacific species (Bertsch, 1977), Rudman (1983, 1984) transferred the tropical Indo-Pacific species *M. mariei* (Crosse, 1872), *M. festiva* (Angas, 1864), *M. macropa* Rudman, 1983, and *M. multituberculata* (Baba, 1953) to this genus. Since then, four additional species have been added to this group (Ortea et al., 1996), including the western Atlantic species *M. kempfi* (Ev. Marcus, 1971) and *M. molloi* Ortea and Valdés, 1996, and the eastern Atlantic species *M. francoisae* (Bouchet, 1980) and *M. garciagomezi* Ortea and Valdés, 1996.

Recently, Johnson and Gosliner (2012), based on molecular data, reorganized the classification of the Chromodorididae and found that the traditional group *Mexichromis* is paraphyletic. According to this new scheme, the eastern Pacific and Caribbean species *M. porterae* (Cockerell, 1901) and *M. kempfi* are transferred to *Felimare* Marcus and Marcus, 1967 along with other eastern Pacific and Atlantic species previously assigned to *Hypselodoris* Stimpson, 1855, whereas *Mexichromis* is maintained for *M. antonii*, the type species, as well as species previously assigned to *Durvilledoris* Rudman, 1984 and *Pectenodoris* Rudman, 1984, and all the tropical Indo-Pacific species of *Mexichromis*.

Although not explicitly tested in their phylogenetic analysis, Johnson and Gosliner (2012) hypothesized that most Atlantic species traditionally assigned to *Mexichromis* likely belong to *Felimare*, including *M. francoisae*, *M. molloi*, whereas eastern Pacific species belong to *Mexichromis*, including *M. tica* Gosliner, Ortea and Valdés, 2004 and *M. tura* (Marcus and Marcus, 1967).

In this paper, a new species of Atlantic chromodorid nudibranch is described based on specimens collected in the Yucatan Peninsula, Mexico. The external morphology and anatomy of this new species is consistent with those of the group traditionally defined as *Mexichromis*, but now considered *Felimare* (Johnson and Gosliner 2012).

MATERIALS AND METHODS

Collection and Preservation: The Campeche Bank is composed of small reefs and cays located in the northwestern sector of the Yucatan Peninsula. The bank reaches 60 m depth (Spalding, 2004). The specimens here studied were collected by hand in the Madagascar Reef, within the Campeche Bank (Ortigosa-Gutiérrez, 2009) as part of a multidisciplinary project aiming to describe the diversity of the main groups of invertebrates (corals, echinoderms, crabs, and shrimps) that inhabit some reefs of the Campeche Bank. The Madagascar Reef is located 40 km offshore and ranges in depth from 4 to 14 m (Zarco-Perelló, 2008). All the specimens were photographed alive, then relaxed with clove oil, and fixed and preserved in absolute ethanol. The type material is deposited in the collections of the Colección Nacional de Malacología, Instituto de Biología, Universidad Nacional Autónoma de México (CNMO) and the Natural History Museum of Los Angeles County (LACM).

Morphological Examination: The specimens were dissected and the reproductive system examined and drawn using a dissecting microscope with camera lucida. The buccal mass of one individual was removed and dissolved in 10% sodium hydroxide, and the radula and jaw examined using a scanning electron microscope (SEM) Hitachi S-3000N at the LACM.

DNA Extraction: DNA extraction was performed using either a hot Chelex® protocol or the DNeasy® Blood and Tissue Kit (Qiagen). Approximately 1–3 mg of the foot was cut into fine pieces for extraction for both protocols. For the Chelex® extraction, the foot tissue was rinsed and rehydrated using 1.0 mL TE buffer (10 mM Tris, 1 mM EDTA, pH 8.0) for 20 minutes. A 10% (w/v) Chelex® 100 (100–200 mesh, sodium form, Bio-Rad) solution was prepared using TE buffer. After rehydration, the tissue mixture was then centrifuged, 975.00 µL of the supernatant was removed, and 175.00 µL of the Chelex® solution was added. Samples were then heated in a 56°C water bath for 20 minutes, heated in a 100°C heating block for 8 minutes, and the supernatant was used for PCR. The DNeasy protocol supplied by the manufacturer was followed, with some modifications. The elution step was modified such that the first elution was collected using 100.00 µL of Buffer AE and was allowed to incubate at room temperature for 5 minutes before centrifugation. In a new test tube, a second elution step was conducted using 200.00 µL of Buffer AE and was also allowed to incubate at room temperature for 5 minutes before centrifugation. The first elution was used for PCR.

PCR Amplification and Sequencing: Palumbi's universal 16S primers (Palumbi, 1996), as well as internal primers for 16S designed for another group of opisthobranchs (Ornelas-Gatdula et al., 2011) were used to amplify the regions of interest. Multiple attempts to obtain CO1 or complete 16S sequences using different primers were unsuccessful.

The master mix was prepared using 34.75 µL H_2O, 5.00 µL Buffer B (ExACTGene, Fisher Scientific), 5.00 µL 25 mM $MgCl_2$, 1.00 µL 40mM dNTPs, 1.00 µL 10mM primer 1, 1.00 µL primer 2, 0.25 µL 5 mg/mL Taq, and 2.00 µL extracted DNA. Reaction conditions were as follows: an initial denaturation for 2 min at 94°C, 35 cycles of (1) denaturation for 30 sec at 94°C, (2) annealing for 30 sec at 50°C, and (3) elongation for 1 min at 72°C, and a final elongation for 7 min at 72°C. PCR product yielding a band of appropriate size, each approximately 250 bp in length, for 16S (16Sar-L + 16Sbr-FAP) was purified using the Montage PCR Cleanup Kit (Millipore). Cleaned PCR samples were quantified using a NanoDrop 1000 Spectrophotometer (Thermo Scientific). Each primer was diluted to 2.0 pmol/µL for sequencing with the PCR products. PCR products were diluted to 6.0 ng/µL. Samples were sequenced at the City of Hope DNA Sequencing Laboratory (Duarte, CA) using chemistry types BigDye V1.1.

Phylogenetic Analyses: Sequences were assembled and edited using Geneious Pro 4.7.4 (Biomatters Ltd.). Geneious was also used to extract the consensus sequence between the primer regions and to construct the alignment for each gene using the default parameters. A total of 250 bp were amplified from the new species and used for the phylogenetic analyses (GenBank accession number JX101321). For comparison purposes, several GenBank sequences belonging to *Mexichromis* (as defined by Johnson and Gosliner, 2012) were downloaded from GenBank: *Mexichromis antonii* (EU982800), *Mexichromis maeropa* (EF534050), *Mexichromis mariei* (EF534049), *Mexichromis festiva* (EF534051), *Mexichromis aurora* (EU982805), *Mexichromis trilineata* (EU982806), *Mexichromis lemniseata* (EU982790), and *Mexichromis similaris* (EF534055), and so were sequences belonging to *Felimare* (as defined by Johnson and Gosliner, 2012): *Felimare orsinii* (AJ225189), *Felimare villafranca* (AF249237), *Felimare bilineata* (EF534052), *Felimare californiensis* (EU982796), *Felimare pieta* (AF249238), *Felimare picta verdensis* (HM162594), *Felimare ruthae* (EU982799), *Felimare kempfi* (EF534047), *Felimare porterae* (EF534067). *Hypselodoris infuscata* (FJ917426) was selected as the outgroup.

The Akaike Information Criterion (Akaike 1974) was executed in MrModeltest v2.3 (Nylander 2004), to determine the best-fit model of evolution. MrModeltest selected GTR+I+G as the best-fit evolutionary model for the data set and estimated the following parameters: Base frequencies (A = 0.3623, C = 0.1202, G = 0.1679, T = 0.3496); Rate matrix ([A-C] = 0.9228, [A-G] = 9.0170, [A-T] = 3.1131, [C-G] = 0.1367, [C-T] = 9.2412); Proportion of invariable sites = 0.3260; Gamma distribution shape parameter = 0.5376. The resulting MrBayes block model line was: lset nst=6 rates=invgamma.

A Bayesian analysis was executed in MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001). The Markov chain

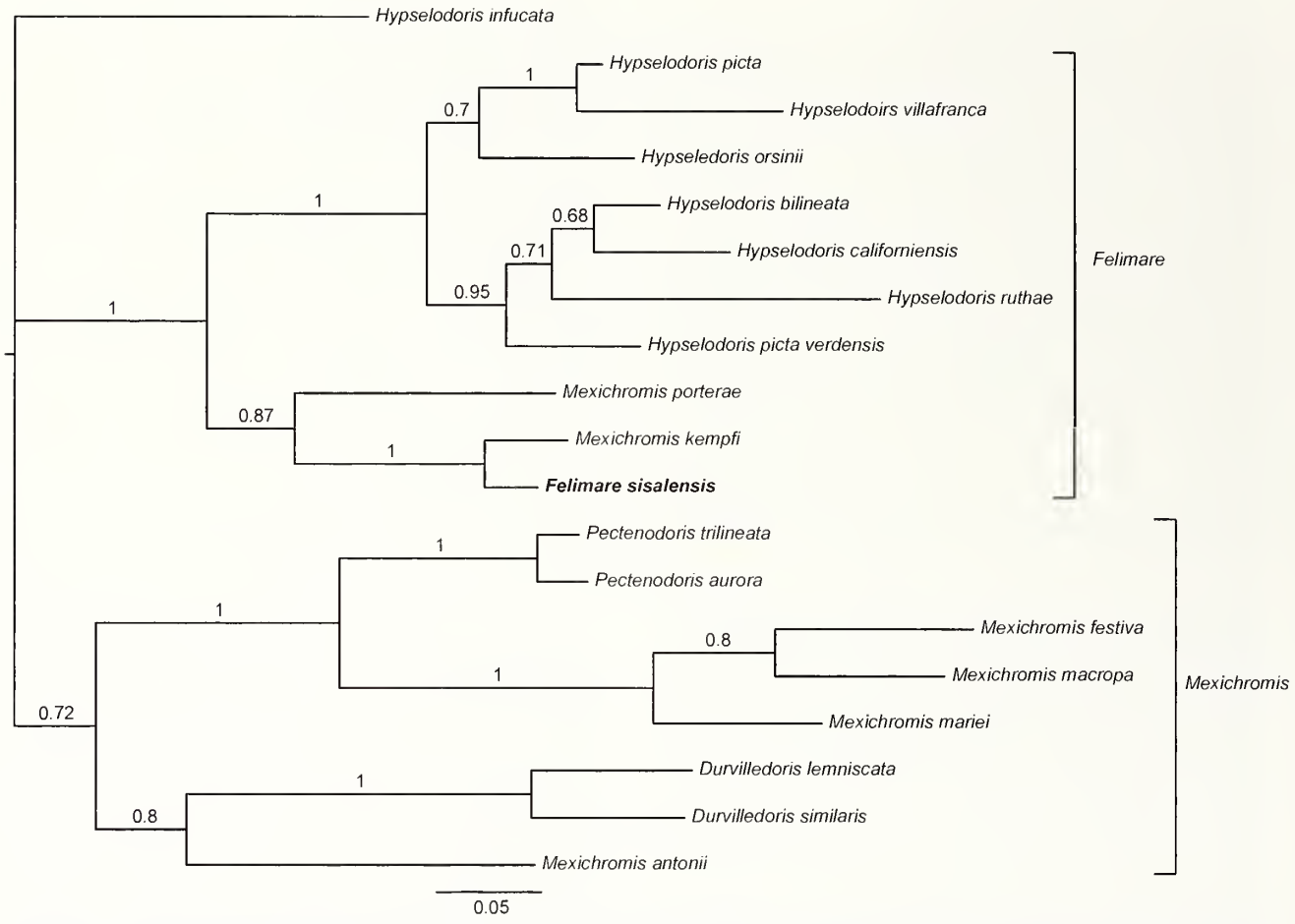

Figure 1. Bayesian tree of 16S sequences. Posterior probabilities are shown only for nodes with values over 0.5. Binominal combinations are the same as used in GenBank, reflecting the established nomenclature before Johnson and Gosliner (2012).

Monte Carlo analysis was run with two runs of six chains for ten million generations, with sampling every 100 generations. All other settings remained in the default. The default 25% burn-in was applied before constructing majority-rule consensus tree. The remaining 150,000 trees were used to construct majority rule consensus trees and calculate posterior probabilities. All clades and support values are shown in the resulting phylogenies. All posterior probabilities are mapped on all trees.

RESULTS

Molecular Data (Figure 1): The Bayesian consensus phylogram (Figure 1) is consistent with the results obtained by Johnson and Gosliner (2012) despite the fact that only one gene was analyzed, although it lacks support in several areas. This phylogeny confirms that *Felimare* is monophyletic (posterior probability = 1.0) and includes Atlantic species previously included in *Hypselodoris* and *Mexichromis* as well as *F. porterae*. Within *Felimare*, species with bicuspid radular teeth (previously classified as *Hypselodoris*) are also monophyletic (posterior probability = 1.0), whereas eastern Pacific and Atlantic species previously classified as *Mexichromis* are clustered in a poorly supported clade. The new species described herein is in this group, confirming the morphological hypothesis of classification proposed in this study.

The rest of the species included in the analysis (formerly *Pectenodoris*, *Durvilledoris* and Indo-Pacific and one eastern Pacific *Mexichromis*) are not supported as monophyletic, but both sample size and gene coverage are too limited to reach any conclusion about the classification of larger groups of the Chromodorididae.

This analysis confirms the position of the new species here described in *Felimare*. It also shows that this species appears to be sister to *F. kempfi* (posterior probability = 1.0), but these two species are genetically distinct in the 16S gene. In the short fragment obtained (250 bp) there were 96.6% of identical sites between the new species and *F. kempfi* which is equivalent to level of sequence similarity between other sister species of Chromodorididae; in the same fragment there were 97.0% of identical sites between *M. aurora* and *M. trilineata*.

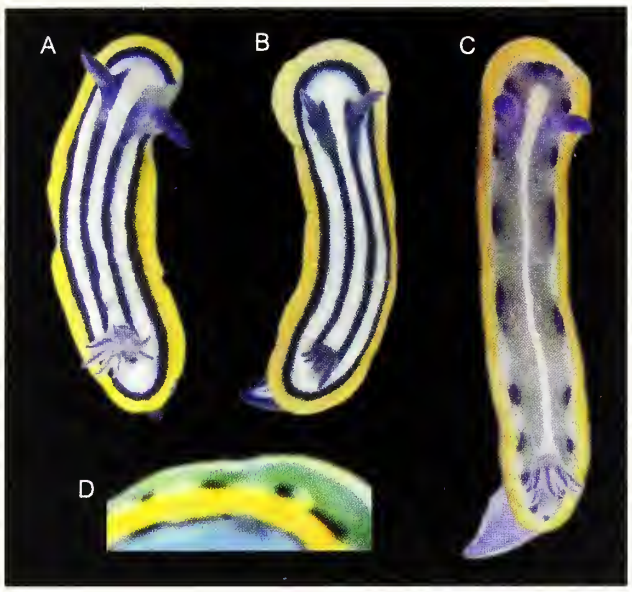

Figure 2. Photographs of live animals. A. Dorsal view of a paratype of *Felimare sisalensis* sp. nov., 11 mm long (LACM 3223), B. Dorsal view of the holotype of *Felimare sisalensis*, 12 mm long (CNMO 3037). C. Dorsal view of a juvenile specimen of *Felimare kempfi* from Campeche Bank, 14 mm long. D. Lateral view of the mantle margin of a juvenile specimen of *F. kempfi* (7 mm long) showing the characteristic black spots.

Morphological Data (Figures 2A–B, 3, 4): The examination of the morphological data conformed that the material here examined represents a new species. The following sections contain the formal description.

SYSTEMATICS

Chromodorididae Bergh, 1981

Felimare

***Felimare sisalensis* new species (Figures 2A–B, 3, 4)**

External Morphology (Figures 2A-B): The body is opaque white with two blue lines that run from each rhinophore to the gill, surrounding it. The mantle edge is surrounded by a yellow band, followed by a thinner blue band. The branchial leaves and rhinophores are blue and retract into pockets. There are nine unnipinnate branchial leaves. The foot sole is opaque white and is surrounded by a blue line. The mantle margin contains one band of small, rounded mantle glands, except for the anterior end of the body.

Reproductive system (Figure 3): The deferent duct is wide and short, followed by a long and narrow prostate. The vagina is short and narrow. The uterine duct connects into the vagina. The bursa copulatrix is large and oval in shape. The seminal receptacle is somewhat elongated and connects into the vagina, at the base of

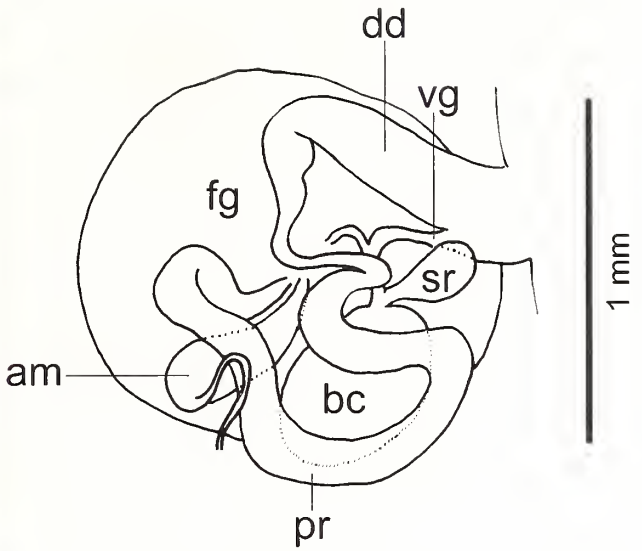

Figure 3. Reproductive system of a paratype of *F. sisalensis* (CNMO 2981). Abbreviations: **am:** ampulla; **bc:** bursa copulatrix; **dd:** deferent duct; **fg:** female gland complex; **pr:** prostate; **sr:** seminal receptacle; **ud:** uterine duct; **va:** vagina; **vg:** vestibular gland.

the bursa copulatrix. The ampulla is relatively short, and straight, with no visible folds. The female gland complex is large, almost the same size that the rest of the reproductive systems. A vestibular gland was not observed, but due to the small size of the reproductive systems it possible that it was overlooked.

Radula and Jaw (Figure 4): The radular formula is 38 × 20.0.20 in a paratype (CNMO2981). There are no rachidian teeth. All lateral teeth are similar in shape and size, with no clear distinction between inner, mid and outer lateral teeth. All teeth are hook-shaped, elongate, with 4-6 denticles. The jaw consists of numerous short, tricuspid rodlets.

Type Material: HOLOTYPE: 12 mm long (CNMO 3037). PARATYPES: 1 specimen 11 mm long (LACM 3223) and 1 specimen 12 mm long (CNMO 2981).

Type Locality: Madagascar Reef, Campeche Bank, Yucatan, Mexico (21°26′28.3″ N, 90°17′22.8″ W), 4 September 2007, 7 m depth. All specimens were collected on green algae.

Geographic Distribution: This species has only been collected on Madagascar Reef, Campeche Bank, Yucatan, Mexico.

Etymology: The species is named in honor of the village of Sisal, Yucatan, Mexico, were the Umdi-Sisal, UNAM station is located.

DISCUSSION

Among the Atlantic species of *Felimare*, only four (those previously assigned to *Mexichromis*) have radular teeth

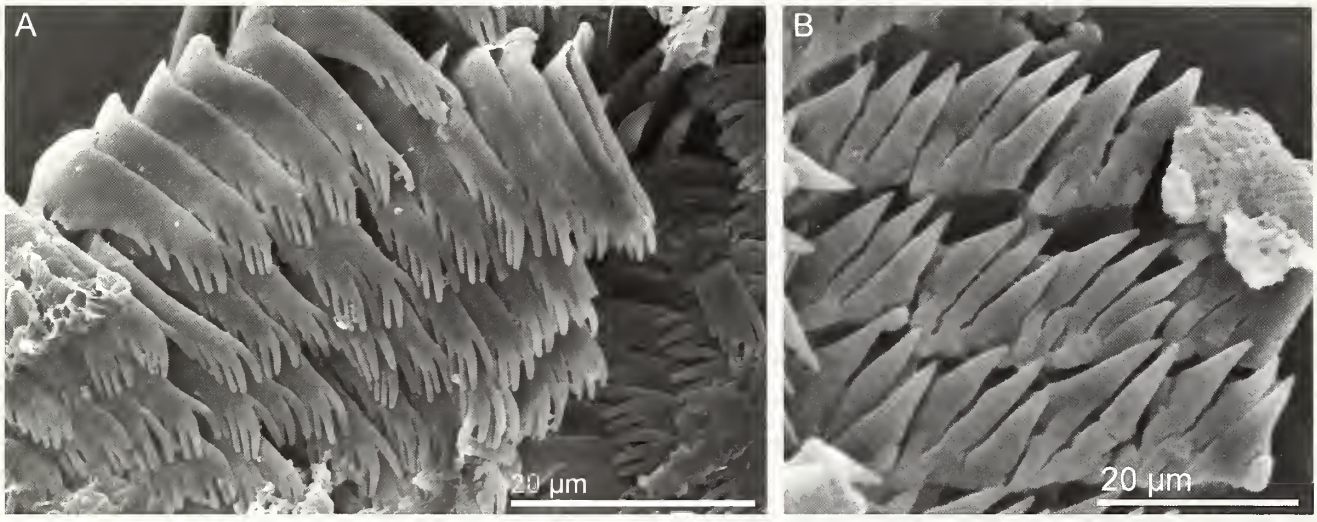

Figure 4. Scanning electron micrographs of a paratype of *F. sisalensis* (CNMO 2981). A. Outer teeth. B. Jaw rodlets.

with all denticles similar in size (non bicuspid) and short jaw rodlets with more than two cusps. These species are *Felimare kempfi*, *F. molloi*, *F. garciagomezi*, and *F. francoisae*. Additionally, molecular data confirms a closer relationship between these species versus species of *Felimare* with bicuspid teeth. Thus, the new species *F. sisalensis*, which has a similar radular and jaw morphology, is compared only to Atlantic species of *Felimare* with non-bicuspid teeth.

All *Felimare* species previously assigned to *Mexichromis* are very uncommon, with no more than eight specimens found per survey even in the case of *F. kempfi* (Meyer, 1977), which is the most common species. Most of these *Felimare* species have restricted geographic ranges. *Felimare francoisae* has been reported only for Cape Verde and Senegal (Bouchet and Ortea, 1980; Ortea et al., 1996). The material from Ghana assigned to *Hypselodoris tricolor* by Edmunds (1981) was described as the new species *M. garciagomezi* by Ortea et al. (1996), because of its distinct external coloration, radula and jaw morphology. This species has not been collected ever since Edmunds's (1981) record. *Felimare molloi*

Table 1. Character comparison of Atlantic species of *Felimare* traditionally assigned to *Mexichromis*.

Species	Mantle Glands	Jaw rodlets (number)	Radular formula	Branchial leaves	Geographic range	References
F. francoisae	On anterior and posterior ends of body	3–4	45×30.0.30	12	Senegal and Cape Verde	Bouchet & Ortea, 1980; Ortea, 1988; Ortea et al., 1996
F. garciagomezi	On each side of rhinophores and on the posterior end of body	3–4	23×12.0.12	6 (8 mm specimen) 4 (3.5 mm specimen)	Ghana	Edmunds, 1981
F. kempfi	not observed	3–5	50×35.0.35	9	USA (Florida), Mexico (Quintana Roo), Panama, Costa Rica, Colombia, Brazil, Puerto Rico	Marcus, 1970; Meyer, 1977; Collin et al., 2005; Valdés et al., 2006; Ardila, et al., 2007; Ortigosa Gutiérrez, 2009
F. molloi	On each side of rhinophores and on the posterior end of body	4	28×17.0.17	10	Isla Picuda (Venezuela)	Ortea et al., 1996
F. sisalensis	All around except for anterior end	3–4	32×20.0.20	9	Mexico (Yucatán)	Present study

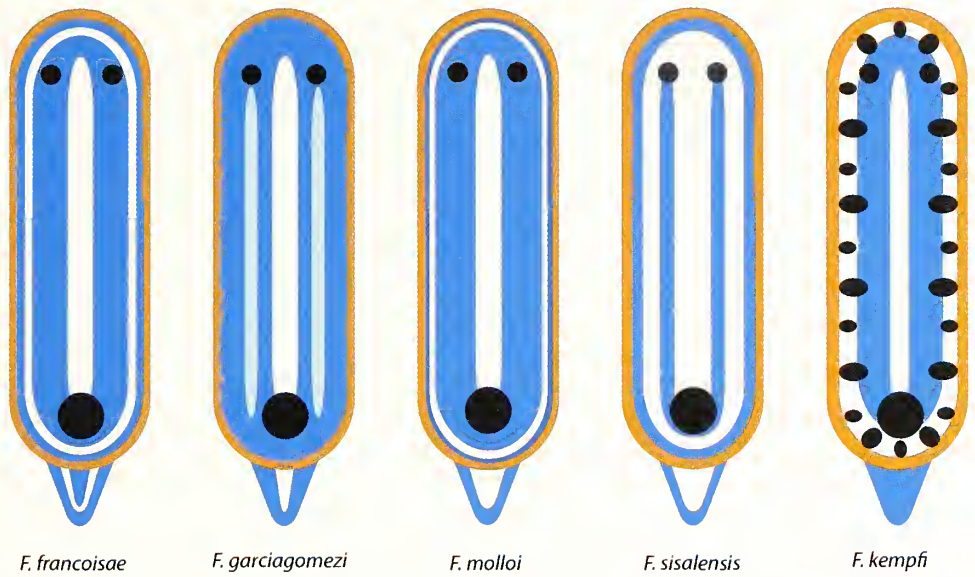

Figure 5. Schematic representation of the color pattern of the Atlantic species of *Felimare* previously assigned to *Mexichromis*.

was originally described based on a single specimen collected in Isla Picuda, Venezuela (Ortea et al., 1996) and never cited again. *Felimare kempfi* is the only species with a relatively broad geographic range including Florida, Mexico, Panama, Costa Rica, Puerto Rico, and Brazil and also in two reefs of the Campeche bank (Table 1). All these species seem to live in shallow waters; the deepest record is for *F. kempfi* in Brazil, at 37 m depth (Marcus, 1971).

Felimare sisalensis can be distinguished easily from those other four species by its external coloration (Figure 5). *Felimare kempfi* is a primarily blue species with a longitudinal white band that runs from between the rhinophores to the gill and a series of elongate black spots on each side of this band, whereas in *F. sisalensis* is mainly white with two blue lines that run from each rhinophore to the gill. Ortigosa-Gutiérrez (2009) reported specimens of *F. kempfi* collected from another reef of the Campeche Bank and similar in size to the type material of *F. sisalensis* (7 and 12 mm long), and the black spots are visible (Figure 2C–D). Valdés et al. (2006) suggested the possibility that *F. molloi* could be a synonym of *F. kempfi*, which would lack black spots as juveniles, but Ortigosa-Gutiérrez's (2009) record suggests that *F. molloi* is indeed a distinct species. *Felimare molloi* has also a white band that runs from between the rhinophores to the gill and instead of the black spots of *F. kempfi*, it has a blue band surrounded by irregular areas of white color. *Felimare garciagomezi* is almost completely blue, with a central white line that runs from the middle of the rhinophores to the gill and two shorter pale blue lines on each side of the central line that do not surround the rhinophores.

The radular and jaw morphology of *F. kempfi* and *F. sisalensis* are very similar, both species lack rachidian teeth, and the outer radular teeth have 6 cusps; the jaw rodlets have 3–4 cusps in both species (Table 1). The radula of the eastern Atlantic species *F. francoisae* is different from that of *F. sisalensis* as it has more cusps on the outer radular teeth (10–11) and the jaw rodlets have 3–6 cusps instead of 3-4 in *F. sisalensis*. Finally *F. garciagomezi* has finely denticulate outer radular teeth (Edmunds, 1981) and jaw rodlets with 3–4 cusps (Table 1).

The only two species for which the reproductive system has been described and illustrated are *F. francoisae* (in Bouchet and Ortea, 1980; Ortea et al., 1996) and *F. molloi* (in Ortea et al., 1996). The reproductive system of *F. sisalensis* is clearly distinguishable from that of *F. francoisae* and *F. molloi* because the seminal receptacle is not connected directly into the bursa copulatrix as in these two species. Additionally, in *F. sisalensis* the deferent duct is wider than that of *F. francoisae*. A vestibular gland was not observed in *F. sisalensis*, but it was reported in *F. francoisae* and *F. molloi* by Ortea et al. (1996).

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LITERATURE CITED

Aikake, H. 1974. A new look at the statistical model identifications. IEEE Trans Auto Control 19: 716–723.

Ardila, N.E., D.P. Báez, and A. Valdés. 2007. Babosas y liebres de Mar (Mollusca: Gastropoda: Opisthobranchia) de Colombia. Biota Colombiana 8: 185–197.

Bertsch, H. 1977. The Chromodoridinae nudibranchs form the Pacific Coast of America. Part I. Investigative methods and supra-specific taxonomy. The Veliger 20: 107–118.

Bouchet, P. and J. Ortea. 1980. Quelques Chromodorididae bleus (Mollusca,Gastropoda, Nudibranchiata) de l'Atlantique Oriental. Annales de l'Institut Océanographique 56: 117–125.

Collin, R., M.C. Diaz, J. Norenburg, R.M. Rocha, J.A. Sanchez, A. Schulze, M. Schwartz, and A. Valdés. 2005. Photographic Identification Guide to Some Common Marine Invertebrates of Bocas Del Toro, Panama. Caribbean Journal of Science 41: 638–707.

Edmunds, M. 1981. Opisthobranchiate Mollusca from Ghana: Chromodorididae. Zoological Journal of the Linnean Society 72: 175–201.

Huelsenbeck, J.P. and F. Ronquist. 2001. MrBayes: Bayesian inference of phylogeny. Bioinformatics 17:754-755. doi:10.1093/bioinformatics/17.8.754

Johnson, R. and T.M. Gosliner. 2012. Traditional taxonomic groupings mask evolutionary history: A molecular phylogeny and new classification of the chromodorid nudibranchs. PLoS ONE 7(4): e33479. doi:10.1371/journal.pone.0033479.

Marcus, Ev. 1971. Opisthobranchs from northern Brazil. Bulletin of Marine Science 20: 922–995.

Meyer, K.B. 1977. Dorid Nudibranchs of the Caribbean coast of the Panama Canal Zone. Bulletin of Marine Science 27: 299–307.

Nylander, J.A.A. 2004. MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Ornelas-Gatdula, E., A. DuPont, and Á. Valdés. 2011. The tail tells the tale: taxonomy and biogeography of some Atlantic *Chelidonura* (Gastropoda: Cephalaspidea: Aglajidae) inferred from nuclear and mitochondrial gene data. Zoological Journal of the Linnean Society 163: 1077–1095.

Ortea, J. 1988. Moluscos opistobranquios del Archipiélago de Cabo Verde: Chromodorididae. Publicações Ocassionais da Sociedade Portuguesa de Malacologia 11: 1–16.

Ortea, J., Á. Valdés, and J.C. García-Gómez. 1996. Revisión de las especies Atlánticas de la familia Chromodorididae (Mollusca: Nudibranchia) del grupo cromático azul. Avicennia supplement 1:1–165.

Ortigosa-Gutiérrez, J.D. 2009. Biogeografía de moluscos opistobranquios de Yucatán, México. Master Thesis. Universidad Nacional Autónoma de México, 97 pp.

Palumbi, S.R. 1996. Nucleic acids II: the polymerase chain reaction. In: Hillis DM, Moritz C, Mable BK, eds. Molecular systematics. Sunderland, MA: Sinauer Associates, 205–247.

Rudman, W.B. 1983. The Chromodorididae (Opisthobranchia, Mollusca) of the Indo-West Pacific: *Chromodoris splendida*, *C. aspersa* and *Hypselodoris placida* colour groups. Zoological Journal of the Linnean Society 78: 105–173.

Rudman, W.B. 1984. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. Zoological Journal of the Linnean Society 81: 115–273.

Spalding, M.D. 2004. A guide to the coral reefs of the Caribbean. University of California Press, Berkeley, 256 pp.

Valdés, A., J. Hamann, D.W. Behrens and A. DuPont. 2006. Caribbean Sea Slugs: A Field Guide to the Opisthobranch Mollusks from the Tropical Northwestern Atlantic. Sea Challengers Natural Hystory Books, Gig Harbor, 289 pp.

Zarco-Perelló, S. 2008. Descripción fisiográfica de los arrecifes de Sisal y hábitats del arrecife Madagascar, Yucatán, México. Undergraduate Thesis. Universidad Nacional Autónoma de México, 104 pp.

A new genus and new species of freshwater mussel from the mid Late Triassic rift lakes of eastern North Carolina (Bivalvia: Unionida: cf. Unionidae)

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ABSTRACT

In eastern North America, surface exposures of Triassic basins extend from Nova Scotia southwestward to South Carolina. This interrupted series of half-grabens resulted from early Mesozoic rifting of the supercontinent Pangaea. In south-central North Carolina, the Deep River basin is comprised of the Durham subbasin, the Colon cross-structure, the Sandford subbasin, the Pekin cross structure, and the Wadesboro subbasin. Deposits within the Durham subbasin are recognized as the Chatham Group, part of the Newark Supergroup and form part of a series informally designated as Lithofacies Association II. These strata are considered to be alternating fluvial and lacustrine sediments. Though research on the vertebrate fauna from this lithofacies has been ongoing for over a century, considerably less research, particularly in North Carolina, has been done on the lacustrine invertebrate fauna.

Ongoing field work at a brick-clay quarry in the village of Genlee, Durham County, North Carolina, has yielded three distinct forms of Triassic freshwater bivalves, one is considered here to be of the order Unionoida and the others tentatively a mytiloid in shell outline and a sphaeriid in shell outline. The unionoid specimens are assigned to *Triaslacus* new genus and *Triaslacus carolinesis* new species and are tentatively assigned to the Unionidae. These new specimens are compared with specimens described as belonging to the unionoid families Unionidae, Hyriidae, and Mulleriidae [+Mycetopodidae] from Massachusetts and Pennsylvania. However, none of the North Carolina specimens exhibit the umbonal sculpture exhibited by the northeastern specimens. The North Carolina unionoid specimens lack any evidence of hinge development or umbonal sculpture.

Non-unionoid bivalves are quite rare in these deposits. The bivalve fauna is found in association with ostracods of the genus *Darwinula;* clam shrimp, *Euestheria*, represented by carbonized impressions of the shells; and fish and plant remains. This freshwater environment is preserved in a mudstone or clayey siltstone sediments.

Additional keywords: Unionida, Uniomorphi, Newark Supergroup

INTRODUCTION

Freshwater bivalves in the Order Unionida have been placed in the Cohort Uniomorphi (=Paleoheterodonta), based on shell characters used to identify the sister relationship of Trigonida and Unionida (Weir, 1969; Bieler et al., 2010; Carter et al., 2011). Trigonida and Unionida are considered sister taxa in the Uniomorphi based initially on shell morphology and the presence of nacre. This relationship is supported by DNA analyses (Hoeh et al., 1998; Hoeh et al., 2001; Giribet and Wheeler, 2002; Taylor et al., 2007).

Subdivision of the Unionida has varied over the past hundred years from a single family to six modern families and various included fossil groups (e.g., Haas, 1969; Starobogatov, 1970; Carter et al., 2011). Taxonomic placement of fossil freshwater bivalves in modern extant families and genera is not supported. This practice is fraught with problems of convergence of shell morphology (Ortmann, 1912; Prashad, 1931; Hartman and Bogan, 2009). Allocations of bivalve taxa discussed here are based on shell shape and morphology and are considered tentative until there is a phylogenetic analysis of the modern and fossil Unionida.

History of North American bivalve fossils assigned to the Order Unionida was summarized by Henderson (1935) and more recently reviewed by Watters (2001). Triassic freshwater bivalves described from the eastern United States are primarily from Pennsylvania and Massachusetts (Table 1). North American Triassic freshwater bivalves described from the southwestern United States including Texas, New Mexico, Arizona, California, and Utah, are assigned to Unionidae and Hyriidae (Good, 1998).

Pilsbry (1921, 1926) placed the Triassic freshwater bivalve taxa from the northeastern United States in the modern South American families Mycetopodidae based on similarity of shell shape to the modern genus

Table 1. List of freshwater bivalves from the Triassic of the eastern United States.

Mulleriidae (+Mycetopodidae)
Mycepoda? diliculi Pilsbry in Wanner, 1921, Pennsylvania

Hyriidae
Diplodon borealis Pilsbry in Wanner, 1921; Pilsbry, 1926, Pennsylvania
Diplodon carolus-simpsoni Pilsbry in Wanner, 1921, Pennsylvania
Diplodon pennsylvanicus Pilsbry in Wanner, 1921, Pennsylvania
Diplodon wanneri Pilsbry in Wanner, 1921, Pennsylvania
Diplodon yorkensis Pilsbry, in Wanner, 1921 Richards 1944, Pennsylvania

Unionidae
Unio emersoni Troxell, 1914, Massachusetts
Anoplophora wilbrahamensis Emerson, 1900, Massachusetts [moved to *Unio* by Lull, 1915]
Unionidae sp. Bain and Harvey, 1977; Good, 1995a; Good, 1995b, North Carolina

Trace fossils (Lull, 1915, as Mollusks?; Henderson, 1935, as freshwater mussel trails).
Bisulcus undulatus Hitchcock, 1865, Massachusetts
Trisulcus laqueatus Hitchcock, 1865, Massachusetts

Mycetopoda, and Hyriidae based on radial umbo sculpture, similar to the modern genus *Diplodon*. Remaining taxa were described or moved to the genus *Unio* and assumed to belong in the family Unionidae.

Two trace fossils described by Hitchcock (1865) *Bisulcus undulatus* Hitchcock, 1865 and *Trisulcus laqueatus* Hitchcock, 1865, both from Massachusetts, were described as annelids. *Trisulcus* was listed as a worm track by Lesley (1890), who failed to list *Bisulcus*. Lull (1915, 1917) placed them in Mollusca? noting they differ from worms in being multiple-, double-, or triple-ridged trails. Both of these taxa were listed as possible tracks of freshwater mussels but with no further elaboration by Henderson (1935). There is some doubt that these represent tracks of freshwater mussels and not some other invertebrate.

GEOLOGICAL SETTING

The Deep River Basin, located in east-central North Carolina, resulted from early Mesozoic rifting of the supercontinent Pangaea (Clark et al., 2001). This north to northeast-trending half graben is about 226 km long and averages about 16 km in width (Bain and Harvey, 1977). Deposits of the Deep River Basin consist of varying amounts of conglomerate, sandstone, siltstone, claystone, shale, coal, and small amounts of limestone and chert (Clark et al., 2001). These deposits are recognized as the Chatham Group, part of the Newark Supergroup as defined by Olsen (1978) and Luttrell (1989). The Deep River Basin is bordered on the east by the Jonesboro fault, a west-dipping, high-angle normal fault (Campbell and Kimball, 1923). The Jonesboro fault separates Triassic sedimentary rocks of the basin from the Raleigh metamorphic belt and Carolina zone metavolcanics and metasediments (Clark et al., 2001). Minor faults form the basin's western border, where Triassic sedimentary rocks unconformably overlie Late Proterozoic and Cambrian metavolcanic and metasedimentary rocks (NCGS, 1985). Several minor faults have also been recognized throughout the basin. From north to south, the Deep River Basin is traditionally divided into four substructures: Durham subbasin, Colon cross-structure, Sanford subbasin, and the Wadesboro subbasin (Bain and Harvey, 1977). Some workers also recognize The Pekin cross structure between the Sanford and Wadesboro Basins (Clark et al., 2001).

Bivalves described herein were recovered by North Carolina Museum of Natural Sciences research staff and volunteers in the late 1990s and early 2000s from a brick/clay quarry in Durham County, North Carolina (Figure 1). The quarry is located in the northeast corner of the Green Level 7.5-minute Quadrangle at 35°52′14.12″ N latitude and 78° 53′51.77″ W longitude (coordinates are from Acme Mapper 2.0 http://mapper.acme.com/ on June 10, 2012 using WGS 84) in the village of Genlee, Durham County, North Carolina (Olsen and Huber, 1997). Strata in this quarry occur in the south-central part of the Durham subbasin of the Deep River Basin (Chatham Group of the Newark Supergroup) (Sues et al., 2003a), and form part of a series informally designated as Lithofacies Association II (Hoffman and Gallagher, 1989). Kozur and Weems (2007) placed this lithofacies in the Sanford Formation. The main quarry exposes about 60 m of red, purple and gray fissile to bioturbated massive mudstones interbedded with gray, brown and red arkosic sandstones (Olsen and Huber, 1997) and are considered by Hoffman and Gallagher (1989) to be a series of alternating fluvial and lacustrine facies. The recovery of the vertebrate *Aetosaurus* from the quarry provides a Norian age for the local section (Lucas et al., 1998). However, using conchostracan biostragraphy, Kozur and Weems (2007) determined a latest Tuvalian (Carnian) age for the section. As the conchostracans and unionoid bivalves come from layers well below the layers containing the vertebrates, it is possible that quarry sediments straddle the Carnian/Norian boundary.

A modified version of the exposed section at the quarry is given in Olsen and Huber (1997, fig. 3) and earlier versions of the section are given in Olsen (1977) and Olsen et al. (1989, 1991). From the fluvial facies of this quarry, Parker (1966) and Lucas et al. (1998) described a partial articulated skeleton of *Aetosaurus* (=*Stegomus*). Sues et al. (2003b) also reported an articulated rauisuchian, *Postosuchus* sp., with gut contents consisting of a partial skeleton of *Aetosaurus* (=*Stegomus*), limb bones of a juvenile traversodont, a partial dicynodont digit and a dermal bone of an indeterminate temnospondyl from one of the fluvial facies. Also, from that same lithofacies, beneath the torso of

Figure 1–6. Freshwater bivalves from the mid Late Triassic rift lakes of eastern North Carolina Triangle. **1.** Brick Quarry, Carpenter Plant brick pit. **2.** *Triaslacus carolinesis* holotype, NCSM 9169A, total shell length is 10.54 mm. **3.** *Triaslacus carolinesis*, partaypes, NCSM 10781, internal mold. Total shell length = 9.74 mm. **4.** *Triaslacus carolinesis*, specimen NCSM 11156, Cedar Run, Virginia. Total shell length = 8.94 mm. **5.** Possible Sphaeriidae? NCSM 10525. **6.** Possible Mytilidae? NCSM 10520.

the rauisuchian, Sues et al. (2003a) described an articulated skeleton of sphenosuchian crocodylomorph, *Dromicosuchus grallator*. The bivalves described herein come from one of the lower lacustrine facies. Faunal elements found in association with the bivalves include darwinulid ostracodes; the trace fossil *Scoyenia;* cambarid crayfish; fragmentary and articulated fish; occasional phytosaur teeth; and coprolites (Olsen and Huber, 1997). Also found in association with the bivalves, are conchostracans described by Kozur and Weems (2007) as *Euestheria buravasi*, *Euestheria* sp. cf. *E. hausmanni*, and *Anyuanestheria*? new species.

MATERIALS AND METHODS

All specimens used in this description are housed in the North Carolina State Museum of Natural Sciences, Invertebrate Paleontology section, herein abbreviated NCSM.

Shell measurements were made to the nearest millimeter using digital calipers and included total length and height. Total length was defined as distance between anterior and posterior margins, measured parallel to the hinge line. Shell height is distance between dorsal and ventral margins, measured near the midpoint of the hinge line, perpendicular to shell length.

SYSTEMATIC PALEONTOLOGY

Class Bivalvia
Cohort Uniomorphi (=Palaeoheterodonta of authors)
Order Unionoida

Family cf. Unionidae

Genus *Triaslacus* new genus

Type Species: *Triaslacus carolinensis* new species

Diagnosis: A small edentulous freshwater bivalve, oval in outline, lacking any umbonal sculpture.

Description: *Triaslacus* is distinguished from other fossil unionoid species by a combination of the following characteristics: Apparently thin, somewhat inflated, shell, elliptical outline; hinge teeth absent; umbo only slightly elevated above hinge line; umbo sculpture is absent. *Triaslacus* can be distinguished from other Triassic bivalves from northeastern United States assigned to the Unionida by the following combination of characters. It differs in shell shape from the elongate shell shape assigned to Mulleriidae or the more rectangular shape of species assigned to the Hyriidae. *Triaslacus* appear to have a smooth umbo at or only slightly above the hinge line, while other Triassic bivalve taxa have radial umbonal sculpture and are assigned to the Hyriidae. *Triaslacus* appears to be edentulous.

Distribution: Known from the Late Triassic rift lake deposits in North Carolina and Virginia.

Etymology: The genus name *Triaslacus* stands for the Triassic lake deposits where it was collected.

***Triaslacus carolinensis* new species**
(Figures 2–4)

Unionidae sp.—Bain and Harvey, 1977; Good 1995a; 1995b.

Diagnosis: *Triaslacus carolinensis* is distinguished from all other known Late Triassic unionoid bivalves occurring along the east coast of North America by the oval shell outline in contrast to the elongate shell in species of *Mycetopoda*. It lacks the radial umbonal sculpture of *Diplodon* species and does not have the square shell outline of *Unio emersoni*.

Description: Length to 12.8 mm, height to 7.5 mm; shell thin, moderately inflated, outline oval. Posterior margin narrowly rounded to bluntly pointed. Anterior margin broadly rounded. Dorsal margin straight. Ventral margin convex. Posterior ridge rounded. Posterior slope moderately steep. Umbo broad, moderately inflated, barely elevated above hinge line. Umbo sculpture absent. Pseudocardinal and lateral hinge teeth absent. Umbo cavity wide, shallow.

Comparison with Similar Species: *Triaslacus carolinesis* shells do not resemble the shell referred to as *Mycepoda*? *diliculi* Pilsbry in Wanner, 1921and placed in the Mycetopodidae, which is nowadays considered to be restricted to South America. *Triaslacus carolinesis* does not have the radial umbonal sculpture of those taxa referred to the genus *Diplodon* (Table 1) and, by extension, to the family Hyriidae, today restricted to South America, Australia, New Zealand, and New Guinea. *Diplodon carolussimpsoni* from Pennsylvania is more rectangular in shell shape and has a well-marked posterior ridge. *Unio emersoni* is more elongate is shell outline, larger in maximum shell length and possess large hinge teeth, while *Triaslacus carolinesis* is smaller in size, more oval in shell outline and is edentulous. *Anoplophora wilbrahamensis* is more elongate oval in outline, larger in maximum shell length than *Triaslacus carolinesis* and has a long lateral tooth, while *T. carolinesis* is edentulous.

Type Material: Holotype, NCSM 9169, internal mold, both valves. Paratypes, NCSM 10747, negative relief; NCSM 10757, NCSM 10760, cluster; NCSM 10767, negative relief; NCSM 10769, NCSM 10778, positive relief; NCSM 10781, positive relief; NCSM 10790, positive relief. All from the type locality.

Type Locality: United States, North Carolina, Durham–Wake County, Triangle Brick, Carpenter Plant in the village of Genlee. Northeast corner of the Green Level 7.5′ quadrangle at 35°52′ 14.12″ N latitude and 78°53′ 51.77″ W longitude (coordinates are from Acme Mapper 2.0 http://mapper.acme.com/ on June 10, 2012) (Figure 1).

Other Material Examined: United States, North Carolina, Durham–Wake counties, Triangle Brick, Carpenter Plant: NCSM 5035.1-5035.9 all positive/negative; NCSM 5036, 38 specimens; NCSM 5037.1-5037.9, some are both positive/negative; NCSM 6135, total of 7 specimens; NCSM 10745–10746; NCSM 10748–10756; NCSM 10758–10759; NCSM 10761–10766; NCSM 10768; NCSM 10770–10780; NCSM 10782–10788; NCSM 10791; NCSM 10794–10818; United States, Virginia, Fauquier County, Carriage

Ford, Nokesville. Collector: Robert Weems coll. NCSM 11132–11139; United States, Virginia, Hanover County, Stagg Creek transect, Taylorsville Basin, Hannover Academy Quadrangle, Robert Weems coll.; NCSM 11140–11150; United States, Virginia, Fauquier County, Cedar Run. Catlett Quadrangle, Robert Weems coll., NCSM 11151–11158

Etymology: The species is named for the state of North Carolina, where the species was first collected.

Distribution: Triangle Brick Quarry Carpenter Plant, Gen Lee, Durham–Wake County, North Carolina. Carriage Ford, Nokesville, Fauquier County, Virginia. Stagg Creek transect, Taylorsville Basin, Hannover Academy Quadrangle, Hanover County, Virginia and Cedar Run, Catlett Quadrangle, Fauquier County, Virginia.

Stratigraphy: Mid Late Triassic (Carnian–Norian Stage interval) Newark Supergroup, Lithofacies H.

Habitat: *Triaslacus carolinesis* is found in similar sedimentary deposits bearing similar associated faunal elements in Durham County North Carolina, and Fauquier County, Virginia. Good (1995a,b) suggested the small or "dwarfed" size of the unionoid is due to "environmental conditions not optimum for this group, probably indicating a deep water lacustrine habitat." Small shell size is common in modern unionoids and some species are found at depths over 15 m and they are not dwarfed (Bailey and Green, 1989). The lake environment was likely rather shallow and soft bottomed, containing aquatic vegetation, associated fish, ostracods and clamshrimp. The latter species is found in lacustrine facies suggesting soft-bottomed deposits in quiet water similar to habits of the common modern thin-shelled eastern North American anodontine, *Utterbackia imbecillis* (Say, 1829).

Order Cardiida?

Family Sphaeriidae?
(Figure 5)

Description: Shell almost round in outline with some valve inflation, reminiseent of modern Sphaeriidae, None of the specimens have exposed hinge plates that would allow for family level confirmation (see Mackie, 2007).

Habitat: Sphaeriids occur today throughout the world in freshwater habitats similar to those described here for Lithofacies H.

Geologic History: Keen (1969) lists Late Jurassic? as the oldest record for the family Sphaeriidae. If correctly identified, this record would extend the geologic range of the family back to the Late Triassic.

Material Examined: NCSM 10521–10524, 10819, 11157, 11158, from Lithofacies H, Triangle Brick Quarry Carpenter Plant, Gen Lee, Durham–Wake County, North Carolina and Cedar Run, Catlett Quadrangle, Fauquier County, Virginia NCSM 11157–11160. Specimens 11157 and 11158 also have *Triaslacus* on the same block.

Cohort Mytilomorphi
Order Mytilida?

Family Mytilidae?
(Figure 6)

Description: Specimens with a mytilid shell shape, with umbo area very anterior and a rather elongate oval shape are tentatively referred to Mytilidae.

Geologic History: This family is reported as occurring from the Devonian to the Recent (Soot-Ryen, 1969).

Material Examined: NCSM10520, 10820–10822, Lithofacies H, Triangle Brick Quarry Carpenter Plant, Gen Lee, Durham–Wake County, North Carolina.

Remarks: Pilsbry (1926) described *Naiadites triassicus* Pilsbry in Wanner, 1926 and *Naiadites wanneri* Pilsbry in Wanner, 1926, recognizing that this genus was known from the Coal Measures [Upper Carboniferous] of Nova Scotia and far earlier than the Triassic deposits these specimens were collected. Weir (1969) placed *Naiadites* in the family Myalinidae.

Good (1995a, b) claimed that the identification of the small associated bivalves from these deposits are non-marine Myalinidae. As Good pointed out, they are not Cyrenidae (+ Corbiculidae), but some appear to resemble Mytilidae (Figure 6) and others Sphaeriidae (Figure 5). This does not, as yet [?], call for a Lazarus distribution between the Pennsylvanian and the Late Triassic.

DISCUSSION

Freshwater bivalves from the Durham subbasin and the Taylorsville Basin of Virginia are described here as a new genus and species of freshwater bivalve tentatively assigned to the family Unionidae. *Triaslacus carolinesis* differs from the Triassic freshwater bivalves described from Connecticut, Massachusetts, and Pennsylvania in shell outline, inflation and umbonal sculpture. *Triaslacus carolinesis* is only tentatively assigned to the Unionidae based on the shell outline, lack of radial umbonal sculpture and lack of hinge teeth. The ambiguity of family assignment is due to rampant shell shape convergence or shell homeomorphy in freshwater bivalves (Ortmann, 1912; Prashad, 1931; Watters, 1994)).

White (1907), writing on the origin of the North American fossil freshwater bivalve fauna before the work of Pilsbry (1921), felt that the modern unionoid fauna was probably derived from the Triassic fauna of the southwestern United States.

Pilsbry (1921) described Triassic freshwater bivalves for the northeast United States and suggested that this fauna is composed of taxa assigned to the modern families

Hyriidae and Myeetopodidae and suggested that probably all of the North Ameriean fossil Triassie freshwater bivalves were related to the South Ameriean fauna. He felt the hyriid mussels would have disappeared with the migration of "Old World forms in the Upper Trias or Jurassic".

Parodiz (1969) followed this line of reasoning and claimed the Hyriidae of the Triassie of North Amcrica migrated into South Ameriea in the Paleocene.

The evolution of freshwater bivalves in North America has most recently been summarized by Watters (2001), who agreed that Hyriidae occurred in North Ameriea in the Triassic. However, Watters does raise the problem of convergence in shell sculpture and notes the laek of shell eharacters to separate these fossils from the modern Hyriidae.

One of the five major extinction events occurred at the end of Triassic. Timing and extent of this extinction event is eontroversial, catastrophie vs. gradual (e.g. Olsen et al., 1987; Palfy et al., 2000; Hallam, 2002; Tanner et al., 2004; Deenen et al., 2010). Taking into consideration terrestrial extinctions at the end of the Triassie and the expanding rift zone along eastern North America, animals living in these rift lakes appear to have been slated for extinction. Triassie freshwater bivalves collected from the rift lakes of the eastern United States most likely represent an extinet radiation and as sueh, may not have any relation to the currently recognized six families in the Unionida and may not represent the origin of any of the modern Unionida families.

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LITERATURE CITED

Bailey, R.C. and R.H. Green. 1989. Spatial and temporal variation in a population of freshwater mussels in Shell Lake, N.W.T. Canadian Journal of Fisheries and Aquatic Sciences 46: 1392–1395.

Bain, G.L. and B.W. Harvey (eds.) 1977. Field guide to the geology of the Durham Triassic basin: Carolina Geological Society Fortieth Annual Meeting 7–9 October 1977: North Carolina Department of Natural Resources and Community Development, Division of Earth Resources, Geology and Mineral Resources Section, 83 pp.

Bieler, R., J.G. Carter, and E.V. Coan. 2010. Classification of Bivalve Families. Pp. 113–133, in: Bouchet, P. and J.-P Rocroi. (2010). Nomenclator of Bivalve Families. Malacologia, 52(2): 1–184.

Campbell, M.R., and K.W. Kimball. 1923. The Deep River coal field of North Carolina: North Carolina Geological and Economic Survey Bulletin 33, 95.

Carter, J.G., C.R. Altaba, L.C. Anderson, R. Araujo, A.S. Biakov, A.E. Bogan, D.C. Campbell, M. Campbell, Chen, J.-h., J.C.W. Cope, G. Delvene, H.H. Dijkstra, Fang, Z.-j., R.N. Gardner, V.A. Gavrilova, I.A. Goncharova, P.J. Harries, J.H. Hartman, M. Hautmann, W.R. Hoch, J. Hylleberg, Jiang, B.-y., P. Johnston, L. Kirkendale, K. Kleemann, J. Koppka, J. Kříž, D. Machado, N. Malchus, A. Márquez-Aliaga, J.-P. Masse, C.A. McRoberts, P.U. Middelfart, S. Mitchell, L.A. Nevesskaja, S. Özer, J. Pojeta, Jr., I.V. Polubotko, J. Maria Pons, S. Popov, T. Sánchez, A.F. Sartori, R.W. Scott, I.I. Sey, J.H. Signorelli, V.V. Silantiev, P.W. Skelton, T. Steuber, J.B. Waterhouse, G.L. Wingard, and T. Yancey. 2011. A synopitical classification of the Bivalvia (Mollusca). Paleontological Contributions Number 4. Kansas University Palcontological Institute. The University of Kansas, Lawrence, Kansas. October 27, 2011, 47 pp.

Clark, T.W., P.J.W Gore, and M.E. Watson. 2001. Depositional and structural framework of the Deep River Triassic basin, North Carolina. In: Hoffman, C.W. (ed.) Fiftieth Annual Meeting Southeastern Section Geological Socicty of America, April 2001, Field Trip Guidebook, pp. 27–50.

Deenen, M.H.L., M. Ruhl, N.R. Bonis, W. Krijgsman, W.M. Kuerschner, M. Reitsma, and M.J. van Bergen. 2010. A new chronology for the end-Triassic mass extinction. Earth and Planetary Science Letters 291: 113–125.

Emerson, B.K. 1900. A new bivalve from the Connecticut River Trias. American Journal of Science (series 4) 10: 58.

Giribet, G. and W. Wheeler. 2002. On bivalve phylogeny: a high-level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. Invertebrate Biology 121: 271–324.

Good, S.C. 1995a. Molluscan paleoccological associations of the Newark Supergroup basins as paleoenvironmental indicators. 1995 Geological Society of America, Abstracts with Programs, Northeastern Section, page 49 (No. 19567).

Good, S.C. 1995b. Taxonomic position of small bivalves from the Newark Supergroup: a unionid dwarf and a nonmarine myalinid. 1995 Geological Society of America, Abstracts with Programs, Northeastern Section, page 49 (No. 19566).

Good. S.C. 1998. Freshwater bivalve fauna of the Late Triassic (Carnian-Norian) Chinle, Dockum, and Delores Formations of the Southwest United States. In: P.A. Johnston and J.W. Haggart (eds.) Bivalves: an eon of evolution – paleobiological studies honoring Norman D. Newell. University of Calgary Press, Calgary, pp. 223–249.

Haas, F. 1969. Superfamily Unionacea. In: R.C. Moore (editor). Treatise on Invertebrate Paleontology. Geological Society of America and the University of Kansas, Part N, Volume 1 [of 3]. Mollusca 6. Bivalvia, pp. N411–N470.

Hallam, A. 2002. How catastrophic was the end-Triassic mass extinction. Lethaia 35: 147–157.

Hartman, J.H. and A.E. Bogan. 2009, Deep time, geologie events, and palcobiogeographie distanee: when is the application of extant genera to fossil continental molluscan species pointless? In: Allmon, W.D., Mikkelsen, P.M., Cronin, K., American Malacologieal Society: Ithaca, Paleontologieal Research Institution Special Publieation 37, p. 13.

Henderson, J. 1935. Fossil non-marine Mollusea of North America. Geological Society of America, Special Papers Number 3. P. vii, 1–313.

Hitehcoek, E. 1865. Supplement to the Ichnology of New England. A report to the Government of Massachusetts, in 1863. Wright & Potter, State Printers, No. 4 Spring Lane, Boston, 96 pp., 20 plates.

Hoeh, W.R., M.B. Black, R. Gustafson, A.E. Bogan, R.A. Lutz, and R.C. Vrijenhoek. 1998. Testing alternative hypotheses of *Neotrigonia* (Bivalvia: Trigonioida) Phylogenetie relationships using Cytochrome C Oxidase Subunit 1 DNA sequenees. Malaeologia 40: 267–278.

Hoeh, W.R., A.E. Bogan, and W.H. Heard. 2001. A phylogenetic perspective on the evolution of morphological and reproductive characteristies in the Unionoida. In: G. Bauer and K. Wäehtler (eds.) "Ecology and Evolutionary Biology of Freshwater Mussels, Unionoida" Ecologieal Studies Vol. 145. Springer Verlag, pp. 257–280.

Hoffman, C.W. and P.E. Gallagher. 1989, Geology of the Southeast Durham and Southwest Durham 7.5 minute Quadrangles, North Carolina: North Carolina Geological Survey Bulletin 92, 34 pp., 1:50,000-seale maps.

Keen, M. 1969 Family Pisidiidae Gray, 1857. In: R.C. Moore (editor). Treatise on Invertebrate Paleontology. Geological Soeiety of America and the University of Kansas, Part N, Volume 2 [of 3]. Mollusca 6. Bivalvia, pp. N669–670.

Kozur, H.W. and R.E. Weems. 2007. Upper Triassie conchostracan biostratigraphy of the continental rift basins of eastern North Ameriea: it's importance for correlating Newark Supergroup events with the Germanic Basin and international geologic time-scale. In: S.G. Lucas and J.A. Spielmann (editors). The Global Triassic. New Mexico Museum of Natural History and Seience Bulletin 41, pp. 137–188.

Lesley, J.P. 1890. A dictionary of the fossils of Pennsylvania and neighboring states named in the reports and catalogues of the survey. Pennsylvania Geological Survey Report P4, volume 3.

Lueas, S.G., A.B. Heckert, and P. Huber. 1998. *Actosaurus* (Archosauromorpha) from the Upper Triassie of the Newark Supergroup eastern United States, and its biochronological signifieanee: Palaeontology 41: 1215–1230.

Lull. R.S. 1915. Triassic life of the Connecticut Valley. State Geologieal and Natural History Survey of Connecticut. Bulletin 24: 1–285.

Lull, R.S. 1917. The Triassic fauna and flora of the Connecticut Valley. U.S. Geological Survey Bulletin 597: 105–127.

Luttrel, G.W. 1989. Stratigraphic nomenelature of the Newark Supergroup of eastern North America: U.S. Geological Survey Bulletin 1572: 1–136.

Maekie, G.L. 2007. Biology of freshwater Corbiculid and Sphaeriid clams of North America. Ohio Biological Survey Bulletin new Series 15(3): 1–436.

North Carolina Geological Survey, 1985, Geologic map of North Carolina: Department of Natural Resources and Community Development, seale 1:500,000.

Olsen, P.E. 1977. Stop1-Triangle Brick Quarry. In: G.L. Bain and B.W. Harvey (eds.) Field Guide to the Geology of the Durham Triassic Basin, Raleigh: Carolina Geological Society, pp. 59–60.

Olsen, P.E. 1978. On the use of the term Newark for Triassic and Early Jurassie rocks in eastern North America: Newsletters on Stratigraphy 7(2): 90–95.

Olsen, P.E., A.J. Froelich, D.L. Daniels, J.P. Smoot, and P.J.W. Gore. 1991. Rift Basins of Early Mesozoie Age. In: Horton, W., ed., Geology of the Carolinas, University of Tennessee Press, Knoxville, pp. 142–170.

Olsen, P.E. and P. Huber. 1997. Field trip stop 3-Triangle Brick Quarry: In: Clark, T.W. (ed.) TRIBI: Triassie Basin Initiative: Abstracts with Programs and Field Trip Guidebook: Duke University, Mareh 21–23, 1997, Field trip Guidebook, pp. 22–29.

Olsen, P.E., R.W. Schlische, and P.J.W. Gore 1989. Field Guide to the teetonics, stratigraphy, sedimentology, and paleontology of the Newark Supergroup, eastern North America. International Geological Congress, Guidebooks for Field Trips T351, 174 pp.

Olsen, P.E., N.H. Shubin, and M.H. Anders. 1987. New Early Jurassic Tetrapod Assemblages Constrain Triassic-Jurassic Tetrapod Extinction Event. Scienee New Series, Vol. 237(4818): 1025–1029.

Ortmann, A.E. 1912. Notes upon the families and genera of the najades. Annals of the Carnegie Museum 8(2): 222–365, plates 18–20.

Palfy, J., J.K. Mortensen, E.S. Carter, P.L. Smith, R.M. Friedman and H.W. Tipper. 2000. Timing the end-Triassie mass extinetion: first on land, then in the sea? Geology 28: 39–42.

Parker, J.M. 3rd. 1966. Triassic reptilian fossil from Wake County, North Carolina: Elisha Mitchell Science Society Journal 82(2): 92.

Parodiz, J.J. 1969. The Tertiary non-marine Mollusca of South Ameriea. Annals of Carnegie Museum, Pittsburgh, PA 40: 1–242.

Pilsbry, H.A. 1921. Mollusks. In: H.E. Wanner. Some faunal remains from the Trias of York County, Pennsylvania. Proceedings of the Academy of Natural Sciences 73: 30–37.

Pilsbry, H.A. 1926. Mollusca, Figures 3,4. In: H.E. Wanner. Some additional faunal remains from the Trias of York County, Pennsylvania. Proceedings of the Aeademy of Natural Sciences 78: 21–28, figures 1–4, plate 3.

Prashad, B. 1931. Some noteworthy examples of parallel evolution in the molluscan faunas of south-eastern Asia and South America. Proceedings of the Royal Society of Edinburgh 51[part 1, no. 8]: 42–53.

Richards, H.G. 1944. Fossil mollusks from the Triassic of Pennsylvania. Proceedings of the Pennsylvania Academy of Science 18: 69–72.

Say, T. 1829. Descriptions of some new terrestrial and fluviatile shells of North America. The Disseminator of Useful Knowledge; containing hints to the youth of the United States, from the School of Industry, New Harmony, Indiana 2(19):291–293, 23 September 1829; 2(20):308–310, 7 Oetober 1829; 2(21):323–325, 21 October 1829; 2(22):339–341, 4 November 1829; 2(23):355–356, 18 November 1829.

Soot-Ryen, T. 1969. Superfamily Mytilacea Rafinesque, 1815. In: R.C. Moore (editor). Treatise on Invertebrate Paleontology. Geologieal Society of Ameriea and the University of Kansas, Part N, Volume 1 [of 3]. Mollusea 6. Bivalvia, pp. N271–N280.

Starobogatov, Ya.I. 1970. Fauna mollyuskov i zoogeographicheskoe raionirovanie kontinental'nykh vodoemov zemnogo shara [Mollusk fauna and zoogeographical partitioning of continental water reservoirs of the world].

Akademiya Nauk SSSR. Zoologischeskii Instituti Nauka, Leningrad, 372 pp., 39 figures, 12 tables [in Russian].

Sues, H.D., P.E. Olsen, J.G. Carter, and D.M. Scott. 2003a, A new crocodylomorph archosaur from the Upper Triassic of North Carolina: Journal of Vertebrate Paleontology 23: 329–343.

Sues, H.D., P.E. Olsen, J.G. Carter, S. Novak, and K. Peyer. 2003b. Life and death in the Late Triassic: An extraordinary tetrapod assemblage from the Newark Supergroup of North Carolina. Journal of Vertebrate Paleontology, 23 supplement to no.3, pp. 102A.

Tanner, L.H., S.G. Lucas, and M.G. Chapman. 2004. Assessing the record and causes of Late Triassic extinctions. Earth Science Reviews 65: 103–139.

Taylor, J.D., S.T. Williams, E.A. Glover, and P. Dyal. 2007. A molecular phylogeny of the heterodont bivalves (Mollusca: Bivalvia: Heterodonta): new analyses of 18S and 28S rRNA genes. Zoologica Scripta 36: 587–606.

Troxell, E.L. 1914. Unios in the Triassic of Massachusetts. American Journal of Science (4) 38(227): 460–462.

Watters, G.T. 1994. Form and function of unionoidean shell sculpture and shape (Bivalvia). American Malacological Bulletin 11: 1–20.

Watters, G.T. 2001. The evolution of the Unionacea in North America, and its implications for the Worldwide fauna. In: G. Bauer and K. Wächtler (eds.) Ecology and Evolution of the Freshwater Mussels Unionoida. Ecological Studies, v. 145. Springer-Verlag, Berlin, pp. 281–307.

Weir, J. 1969. Nonmarine and brackish-water Myalinidae. In: R.C. Moore (editor). Treatise on Invertebrate Paleontology. Geological Society of America and the University of Kansas, Part N, Volume 1 [of 3], Mollusca 6. Bivalvia, pp. N291–295.

White, C.A. 1907. The ancestral origin of the North American Unionidae, or fresh-water mussels. Smithsonian Miscellaneous Collections 48: 75–88, plates 26–31.

Research Note

An albino shell of *Nautilus pompilius* (Cephalopoda: Nautilidae) from the Philippines

ABSTRACT

An albino shell of *Nautilus* is described. The shell is 174.5 mm in diameter with a whorl width at the aperture of 81.9 mm. It bears a black band at the aperture indicating that it is a mature animal. The morphology of the shell conforms to the general species description of *Nautilus pompilius* Linnaeus, 1758, in all respects, except that it lacks any reddish-brown color stripes. The lack of color stripes on the shell is interpreted as a case of albinism, although it is unknown if the soft parts also lacked color. This is the first reported case of an albino *Nautilus* although such shells have periodically cropped up over the years for sale on the internet.

Additional keywords: Albinism, Nautiloidea, Nautilida

INTRODUCTION

All shells of *Nautilus* and *Allonautilus* bear reddish-brown color stripes (Saunders, 1981) although their exact pattern, hue, and intensity vary. The function of the color pattern is interpreted as camouflage (Cowen et al., 1973). The stripes appear in early ontogeny and persist onto the juvenile shell. They disappear on the adoral one-third of the body chamber coincident with the attainment of maturity. We report a specimen of *Nautilus* that lacks any color bands.

REPOSITORY COLLECTION

The specimen is reposited at the American Museum of Natural History (AMNH 275269) and was donated by Mrs. Peter R. Fleischner between 1992 and 1995. According to the accompanying label, the specimen was "collected in traps off Zamboanga, Mindanao, Philippines". However, as described below, the inside surface of the body chamber bears several bryozoan colonies that must have grown after the death of the *Nautilus*, indicating that the shell must have been collected post-mortem.

DESCRIPTION

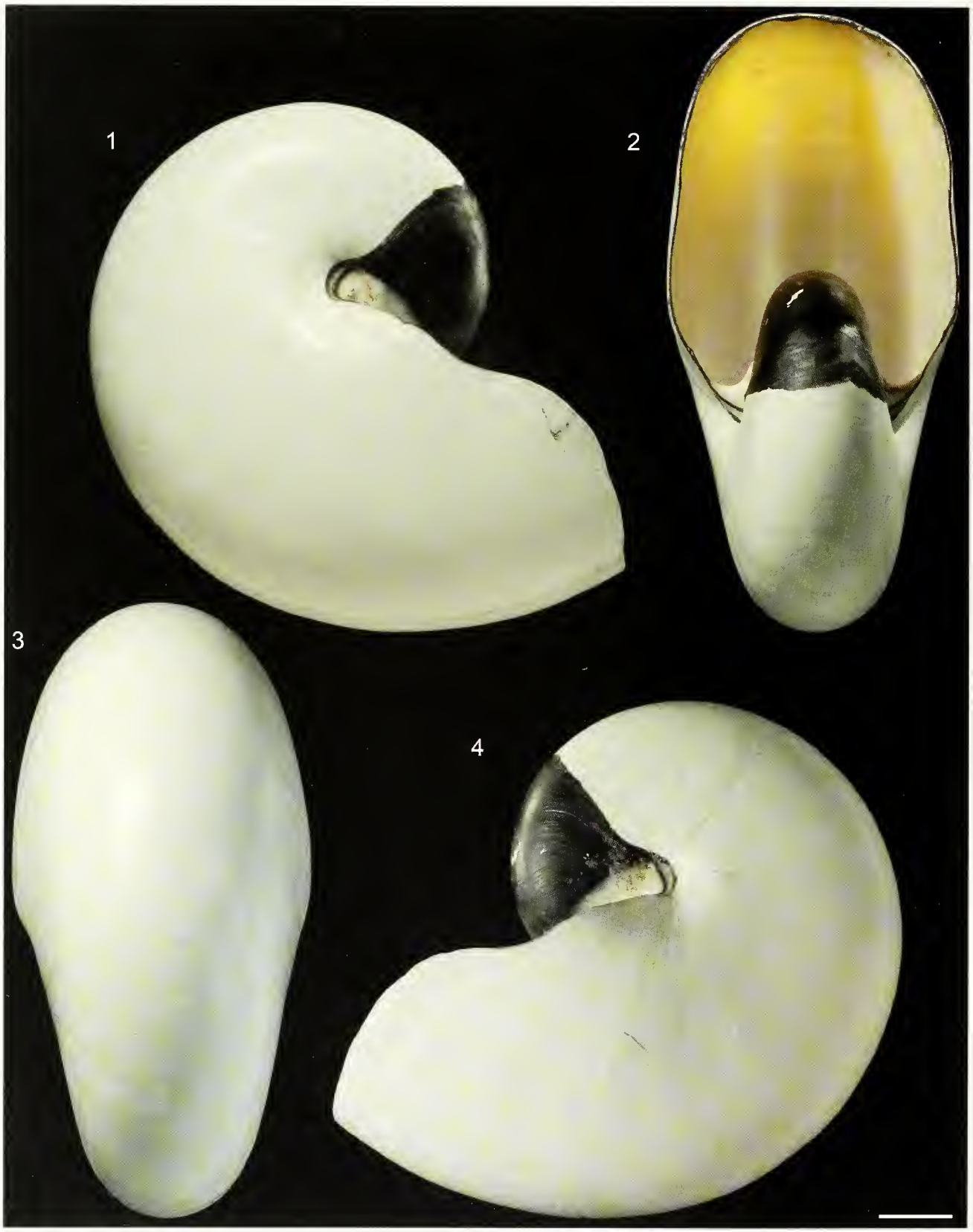
AMNH 275269 is a mature specimen based on the presence of a deep ocular and hyponomic sinus and a thickened apertural margin with a black band 0.5 to 1.5 mm wide (Figures 1–4). The shell conforms to the general description of *Nautilus pompilius* Linnaeus, 1758. It is 174.5 mm in diameter, close to the average size at maturity of this species from the Philippines (165 mm reported in Saunders, 2010: p. 39), with a whorl width at the aperture of 81.9 mm. The umbilicus is small and covered with a well-developed umbilical callus, a hallmark of this species.

The most unusual feature of this specimen is the porcellaneous white color of the shell and the absence of any reddish-brown color stripes. This contrasts with the well-developed black layer on the dorsum. In small areas where the black layer on the dorsal surface of the shell has chipped away, the shell is also white. The specimen does not show any scratches or polishing or any indication of bleaching that would have altered its appearance. Growth lines are prominent with approximately 8 to 16 growth lines/5 mm as measured on the flanks approximately 70 mm adapical of the aperture. Faint longitudinal lirae are also present on the lateral sides and venter of the conch. There are two minor repaired shell breaks, one on the venter on the adoral one-third of the whorl, and one on the right apertural margin. Each is associated with deposits of black material.

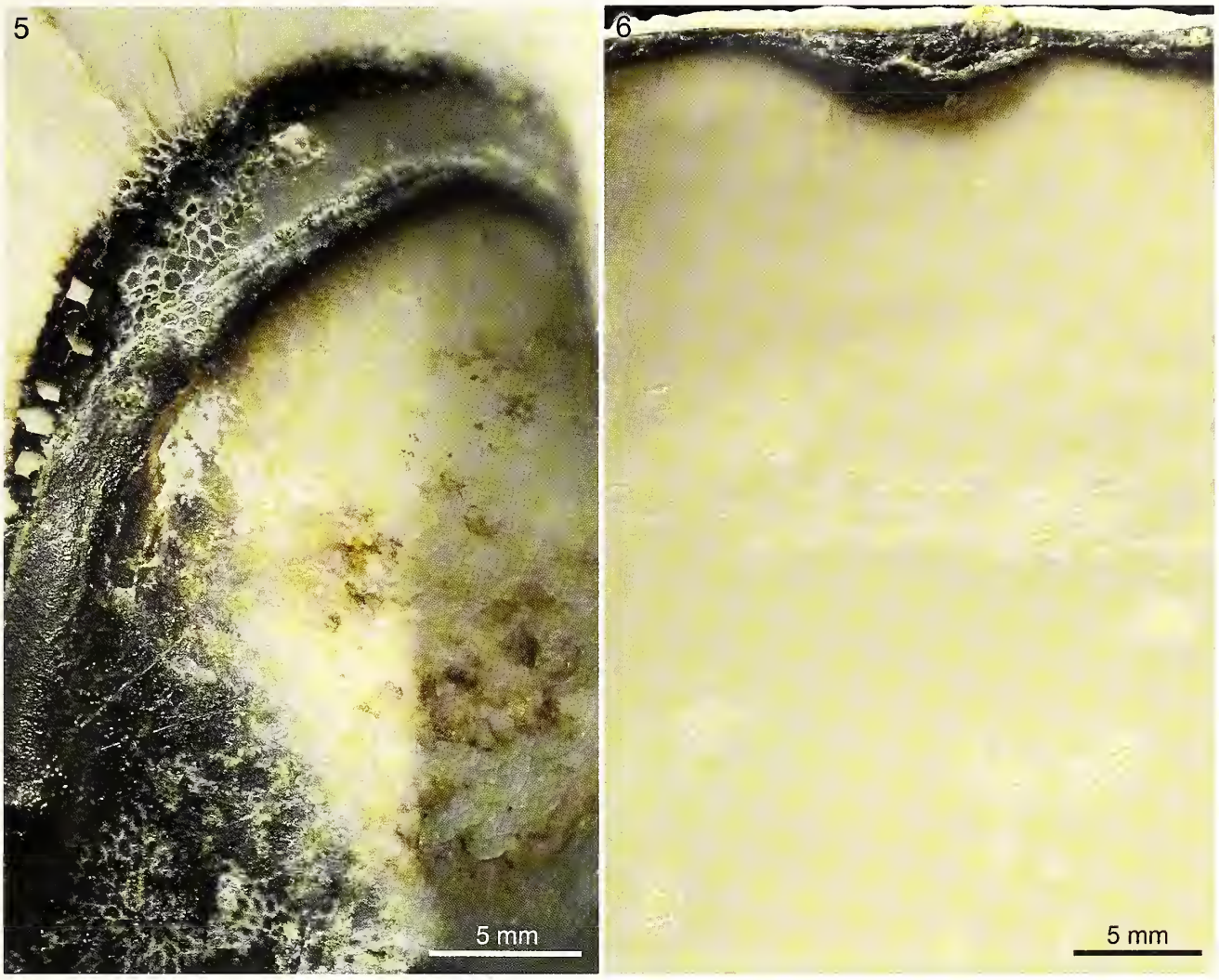
The shell bears evidence of epizoans. A bryozoan colony is covered over by the black layer on the dorsal side. Several traces of bryozoan colonies also appear on and around the umbilical callus (Figure 5). There are also traces of two possible serpulid worm tubes on the left lateral side. Most importantly, the inside surface of the shell near the aperture is covered with several circular to semicircular bryozoan colonies with diameters of up to 15 mm (Figure 6). These bryozoans indicate that the specimen was dead when it was recovered. It was probably floating near the surface and was accidentally caught in a fish trap or net, which is not an uncommon occurrence in the Philippines (Dunstan et al., 2010).

DISCUSSION

Normally, shells of *Nautilus* develop irregular brown to reddish-brown bands or stripes that extend from the umbilicus and branch across the flanks, sometimes coalescing on the venter. In *Nautilus pompilius*, the initial part of the embryonic shell is ivory colored, but at approximately 1 whorl adoral of the apex, the shell develops a pale orange color that subsequently becomes darker. The white and brown color pattern appears gradually, first on the flanks and later on the venter (Arnold et al., 2010). The pattern becomes visible on the flanks about one quarter to one half whorl adapical of the nepionic constriction (the point of hatching). Initially, the boundaries between the color bands are indefinite, but with later growth, they become better defined. After hatching, the color pattern becomes darker reddish brown with sharply defined white bands. In juvenile animals, the color stripes persist to the aperture. The color



Figures 1–4. Mature albino shell of *Nautilus pompilius* (AMNH 275269) from the Philippines. **1.** Right lateral. **2.** Apertural. **3.** Ventral. **4.** Left lateral. Specimen diameter = 174.5 mm.



Figures 5–6. **5.** Bryozoan colonies on the left umbilical callus. **6.** Bryozoan colonies inside the apertural margin, which is marked by a black band (top of photo).

bands disappear on the venter approximately one third whorl adapical of the mature aperture, corresponding to the approximate position of the last septum. This produces a white venter, so that the colored area is restricted to the dorsal part of the shell (Collins and Ward, 2010). Only one specimen of *Nautilus pompilius* was ever reported in which a color band reappears on the white ventral part of a mature shell (Trego, 1993).

The color bands are secreted by pigment secreting cells at the edge of the mantle. The pigment is produced by reddish-brown melanin and is restricted to the outer spherulitic-prismatic part of the shell (Stenzel, 1964). It can be removed by polishing off this layer revealing the iridescent nacreous layer below. Because the pattern involves alternating color and no color and crosses the growth lines, the secretory activities of the cells must sequentially start and stop.

The lack of any color striping on our shell suggests that this animal was an albino. As seen through chips in the black layer, the shell must have been white throughout ontogeny. It is unknown if the hood or other tissues reflected this unusual lack of color. However, it is noteworthy that the black area on the dorsum and the black band at the aperture are present. Both of them consist of black melanin. The black area on the dorsum is secreted by the dorsal part of the mantle covering the earlier secreted part of the shell (Signor, 1985). The black band at the aperture is secreted by the mantle at maturity in association with a termination in shell growth (Collins and Ward, 2010), implying that the cessation of aragonitic secretion is accompanied by the deposit of melanin.

Color striping on *Nautilus* has been interpreted as camouflage to enhance protection from visual predators such as sharks and other fish (see the discussion by Mapes and Davis, 1996). Viewed from above, the normal adult shell exhibits transverse bands of reddish-brown, which serve for counter-shading so that incident light does not illuminate the surface (Cowen et al, 1973).

Additionally, Stenzel (1964) argued that the color bands disrupt the contour of the animal, breaking up its shape and outline. Viewed from below, the adult shell is white, blending in with the surface above.

This albino *Nautilus* would presumably have been more easily detected by visual predators from above or from the side because of its lack of color striping compared to normal animals, thereby reducing its probability of surviving to maturity. Alternatively, the white color may have fooled potential predators because they did not recognize the animal as their usual food item. However, the shell bears two repaired injuries implying that the animal experienced sublethal predation. It is possible that it survived to maturity because it spent most of its time below the photic zone out of sight of visual predators, the preferred habitat of *Nautilus* (Saunders and Ward, 2010).

Recently, we learned that two other albino specimens of *Nautilus pompilius* were recovered from the Philippines (W. B. Saunders, pers. comm., 2012). They were advertised on the internet by a shell dealer, who sold them to a collector. The dealer mentioned that another albino shell had been collected in the area ten years ago. Both of the shells advertised on the internet exhibited heavily modified apertures. One shell, with a diameter of 119.4 mm, was collected by trawling at 400 m off Mindoro, Philippines, and the other shell, with a diameter of 125.8 mm, was recovered by trawling at 350-400 m off Laminusa Island, approximately 600 km south of Mindoro. The occurrence of these shells, plus our own, suggests that albino specimens are rare but present in the population of *N. pompilius* in the Philippines.

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LITERATURE CITED

Arnold, J.A., N.H. Landman, and H. Mutvei. 2010. Development of the embryonic shell of *Nautilus*. In: W.B. Saunders and N.H. Landman (eds.), *Nautilus*: The Biology and Paleobiology of a Living Fossil. Springer, New York, pp. 373–400.

Collins, D. and P.D. Ward. 2010. Adoleseent growth and maturity in *Nautilus*. In: W.B. Saunders and N.H. Landman (eds.) *Nautilus*: The Biology and Paleobiology of a Living Fossil. Springer, New York, pp. 421–432.

Cowen, R., R. Gertman, and G. Wiggett. 1973. Camouflage patterns in *Nautilus*, and their implications for cephalopod paleobiology. Lethaia 6: 201–214.

Dunstan, A., A. Alanis, and J. Marshall. 2010. *Nautilus pompilius* fishing and population decline in the Philippines: a comparison with an unexploited Australian *Nautilus* population. Fisheries Research 106: 239–247.

Mapes, R.H., and R.A. Davis. 1996. Color patterns in ammonoids. In: N.H. Landman, K. Tanabe, and R.A. Davis (eds.) Ammonoid Paleobiology, Topics in Geobiology 13, Plenum Press, New York and London, pp. 103–127.

Saunders, W.B. 1981. The species of *Nautilus* and their distribution. The Veliger 24: 8–17.

Saunders, W.B. 2010. The species of *Nautilus*. In: W.B. Saunders and N.H. Landman (eds.) *Nautilus*: The Biology and Paleobiology of a Living Fossil. Springer, New York, pp. 35–52.

Saunders, W.B., and P.D. Ward. 2010. Ecology, distribution, and population characteristics in *Nautilus*. In: W.B. Saunders and N.H. Landman (eds.) *Nautilus*: The Biology and Paleobiology of a Living Fossil. Springer, New York, pp. 201–212.

Signor, P. 1985. Surficial shell resorption in *Nautilus macromphalus* Sowerby, 1849. The Veliger 28: 195–199.

Stenzel, H.B. 1964. Living *Nautilus*. In: Treatise on Invertebrate Paleontology (Part K) Geological Soeiety America and University of Kansas Press, Lawrence, Kansas, pp. K59–K93.

Trego, K.D. 1993. Band color pattern on the venter of a mature shell of *Nautilus pompilius* Linnaeus, 1758. The Veliger 36: 430–431.

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Corrigendum

In the ACKNOWLEDGMENTS section of the artiele by Lee and Huber (2012), please replace "Ms. Way facilitated the delivery of the images taken by S. Peter Dance of *C. medium* in the Linnean Society Collection" for: "The images of the Linnaean collections available via the Society's website were taken by staff of the NHMUK Science Photography unit in 2008. The A4 sheet whieh aecompanies eaeh set of images is a transeription of the information on the label written by Peter Dance in the mid-1960s for each lot in the collection strongroom."

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The fossil record and phylogeography of the family Cerionidae (Gastropoda: Pulmonata), with the description of a new species from the Pleistocene of Florida

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ABSTRACT

Cerion petuchi, new species, the first record of the genus from the Pleistocene of Florida, is described from Loxahatchee, Florida, from deposits of the Loxahatchee Member of the Bermont Formation (Aftonian Pleistocene). This new species is more similar to *Cerion agassizii* from the Pleistocene of the Creat Bahamas Bank, and to the Recent *Cerion incanum saccharimeta*, from the Florida Keys, than to either of the species from the Late Oligocene—Early Miocene Ballast Point Silex Beds of Tampa, Florida. Data on the geographic distribution and geological age of all known cerionids is compiled and, together with models of the geologic and tectonic history of the Caribbean region, used to construct a hypothesis of the origins, ages, and relationships among the various lineages within the family since the Upper Cretaceous. The early distribution of the family was governed primarily by overland dispersal and vicariance. It is suggested that the significant proliferation of diversity that began during the Pleistocene is due to the increased prevalence of stochastic dispersal of small propagules (either by rafting or hurricane-born) among the islands of the Cuban and Bahamian archipelagos. Sea level changes caused by Pleistocene glaciations amplified diversity by repeatedly and sequentially recombining / hybridizing and isolating neighboring populations. Amplification of diversity would have been greatest on the Creat Bahama Bank, as it had the highest number of islands that were isolated during interglacial periods and conjoined during glaciations.

Additional keywords: Cerion, diversity, zoogeography, vicariance, dispersal

INTRODUCTION

The family Cerionidae has long been known for its exceptional morphological diversity and the profusion of species level taxa in the Recent fauna (e.g., Maynard, 1889–96; Pilsbry, 1901–02; Clench, 1957; Woodruff, 1978). In contrast, the fossil record of the Cerionidae, which extends from the Upper Cretaceous (Roth and Hartman, 1998), is poorly known and represented by comparatively few taxa, most based on rare specimens. A notable exception is in the fauna of the Bahamas, where *Cerion* are locally common in Pleistocene and younger deposits (Hearty and Kaufman, 2009). The geographic and ecological ranges of the family have recently been expanded considerably by inclusion of the genera *Brasilennea* from the Paleocene of the Itaboraí Basin, Brazil (Salvador et al., 2011; Salvador and Simone, 2012), and *Mexistrophia*, from cool, coniferous forests in the highlands of central Mexico (Thompson, 2012).

Within Florida, Cerionidae is represented by two species (one with two subspecies) from the Late Oligocene–Early Miocene Ballast Point Silex Beds of Tampa, Florida, and by a single native Recent species (subdivided into four subspecies) that is confined to the Florida Keys. Thirteen non-native species from the Bahamas, Cuba, Puerto Rico, and Curaçao were intentionally introduced into the Florida Keys and Dry Tortugas between 1912 and 1924 by Paul Bartsch as part of a long-running and well-documented series of experiments (see Harasewych and Strauss, 2006: Table 1). An additional taxon, *Cerion tridentata costellata* Pilsbry, 1946, despite a type locality of Garden Key, Florida, is a hybrid of two of the introduced Cuban species (Harasewych et al., 2011).

One complete and one partial specimen of *Cerion* have recently been discovered in Loxahatchee, Florida, from fossil deposits of Pleistocene age (Bermont Formation). These specimens represent a previously undiscovered species that is described as new and compared to fossil and Recent congeners.

The diversity of the family Cerionidae is reviewed from geographic and temporal perspectives. These results are combined with paleogeographic reconstructions of the Caribbean region (Iturralde-Vinent, 2006) to produce a zoogeographic hypothesis for the dispersal of Cerionidae during the Late-Cretaceous and Cenozoic. A recently published molecular phylogeny of Cerionidae

Table 1. Diversity of species level taxa within the family Cerionidae throughout its geographic and geological range. Data derived from the Cerion website [http://invertebrates.si.edu/cerion/] (Harasewych, 2009).

	TOTAL	Recent	Pleistocene/ Holocene	Pliocene	Miocene	Oligocene	Eocene	Paleocene	Upper Cretaceous
Montana	1								1
Florida[1]	8	4	1			3			
Mexico	3	3							
Little Bahama Bank	11	11							
Great Bahama Bank[2]	263	219	45						
SE Bahama Islands (Isolated Seamounts)[2]	33	32	2						
Turks and Caicos[3]	11	11							
Cuba	153	152	1						
Cayman Islands	16	16							
Hispanola[4]	4	4							
Puerto Rico + Mona[4]	2	2							
Western Virgin Islands[4]	2	1	1						
Aruba, Bonaire, Curaçao[5]	9	9							
Brazil	3							3	
TOTAL	519	464	50			3		3	1

(1) These figures do not include the species introduced into Florida by Bartsch during the first half of the 20th Century (see Harasewych and Strauss, 2006: Table 1), nor does it include *Cerion tridentata costellata*, which, despite a type locality of Garden Key, Florida, is a hybrid of introduced Cuban species (see Harasewych et al., 2011).

(2) Some species were reported both as Recent and Pleistocene.

(3) Clench (1961) synonymized six taxa from Turks Island under *Cerion regina* Pilsbry and Vanatta, 1895.

(4) Gould and Paull (1977) synonymized all living *Cerion* taxa from Hispanola, Mona Island, and Puerto Rico and the Virgin Islands under *Cerion striatellum* Guerin-Meneville, 1829, but retained as separate the fossil *C. rude* (Pfeiffer, 1855) from St. Croix.

(5) The Cerion of Aruba, Bonaire, and Curaçao had been subdivided into four subspecies some with large and dwarf named forms (Baker, 1924). Gould (1984) showed that the four subspecies correspond to geographic subdivisions, while the forms are non-adaptive ecophenotypic variations.

(Harasewych et al., 2011) is used to evaluate portions of this hypothesis.

SYSTEMATICS

Cerion petuchi new species

(Figures 1–11)

Diagnosis: Shell large (to 36 mm), with evenly tapering, conical spire, thick, finely ribbed, with broadly ovate aperture, widely flaring, simply recurved outer lip. Inner lip with parietal region broader than columella, each with a single tooth at mid-length. Umbilicus imperforate.

Description: Shell (Figures 1–9) large (holotype 36.05 mm long, 13.87 mm in diameter), thick, roundly conical in profile, with each whorl slightly broader than the preceding whorl. Protoconch (Figure 10) initially smooth, increasing in diameter from 504 µm to 3.26 mm in 2.6 whorls, with sculpture of 36 weak, evenly spaced axial ribs as broad as the intervening spaces appearing on the final half whorl. Transition to teleoconch (Figure10, **p/t**) marked by an abrupt increase in shell diameter and onset of coarser surface sculpture. Teleoconch of 9⅛ evenly rounded whorls. Suture tightly adpressed. Axial sculpture of multiple (~96 on first teleoconch whorl, ~74 on final whorl) low rounded prosocline ribs (~18° to coiling axis) that generally align with interspaces of prior whorl. Spiral sculpture absent. Aperture expands, deflecting suture adapically ~⅛ whorl prior to formation of thickened and flared terminal lip. Aperture broadly ovate, with the parietal wall forming an angle of 112° with the shorter columella. Single parietal tooth (Figure 11, **par**) emerges from mid-point of parietal callus. A weaker, broader tooth (Figure 11, **col**) recessed along mid-length of columella. Umbilicus imperforate, obscured by expanded terminal lip.

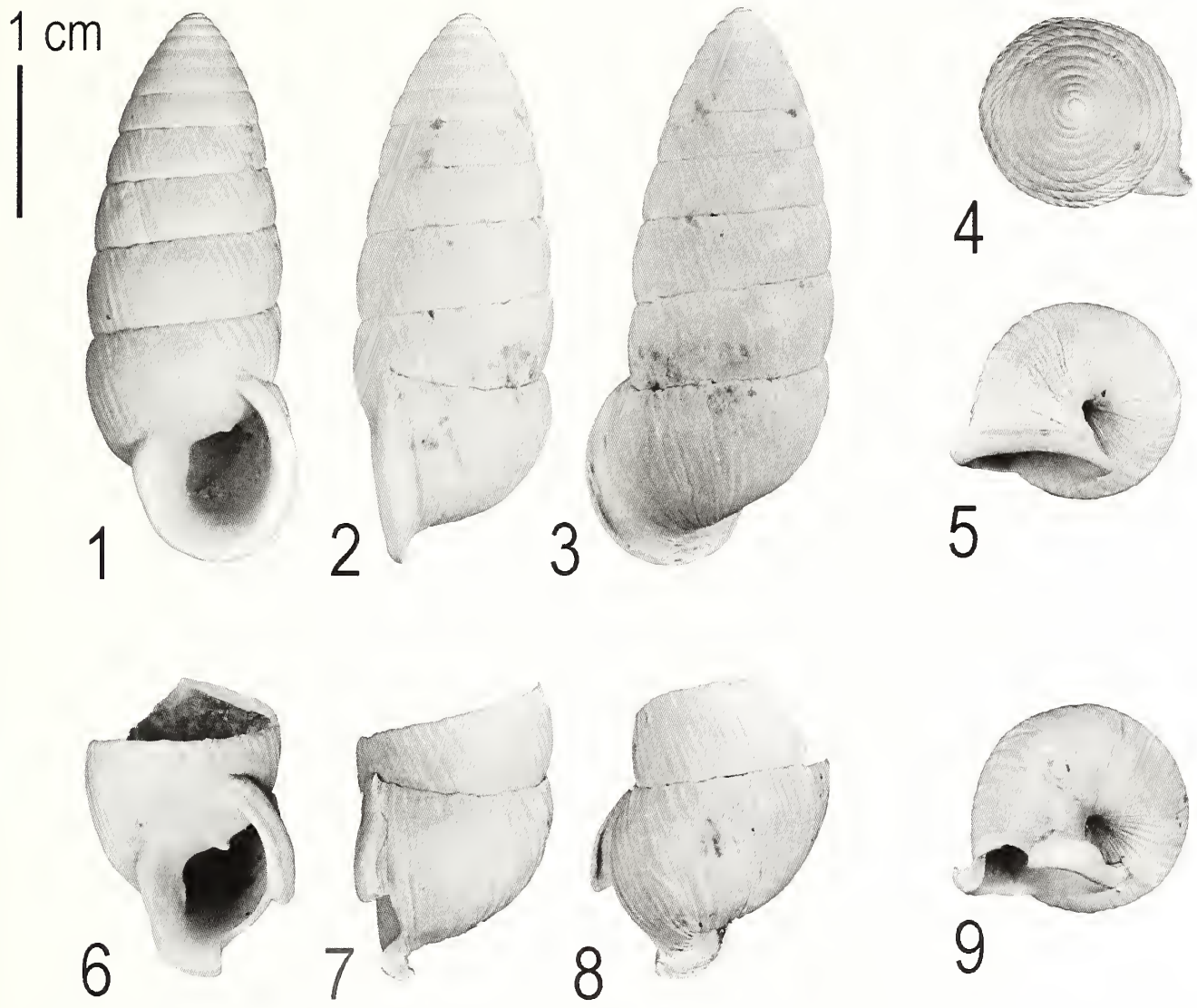
Type Locality: Palm Beach Aggregates, Inc. (old GKK) pit number 7, Loxahatchee, Palm Beach County, Florida [26°42.20′ N, 80°20.97′ W], at 15 m depth.

Stratigraphy: From the Holey Land Member of the Bermont Formation. Aftonian Pleistocene (~1.6 million years before present) (Petuch and Roberts, 2007: 147–162).

Type Material: Holotype, USNM 1191690; Paratype 1, USNM 1191691, both from the type locality.

Distribution: Known only from the type locality. This species was living in the Tomeu Paleoislands, along the northern end of Palm Beach Paleoarchipelago, Loxahatchee Subsea, Okeechobean Sea during the Aftonian Pleistocene (Petuch, 2003: fig. 31).

Etymology: This species honors Dr. Edward J. Petuch, who discovered it, in recognition of his many contributions to our understanding of the Recent and

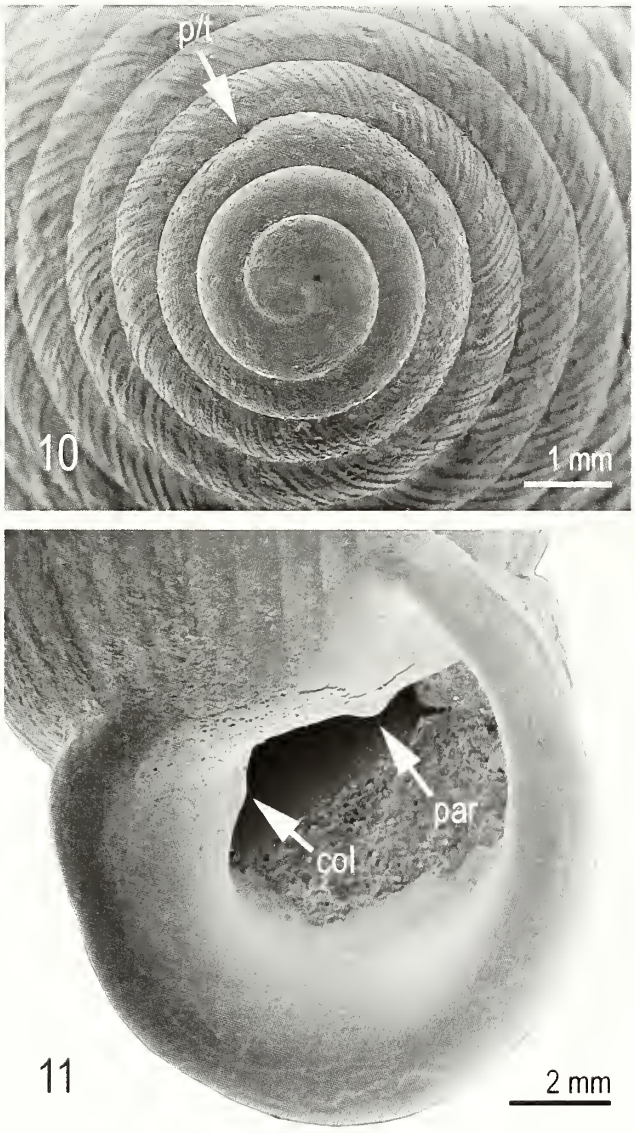


Figures 1–9. *Cerion petuchi* new species. **1.** Apertural, **2.** Lateral, **3.** Dorsal, **4.** Apical and **5.** Anterior views of the holotype (USNM 1191690). **6.** Apertural, **7.** Lateral, **8.** dorsal, and **9.** Anterior views of paratype fragment (USNM (X1191691). Palm Beach Aggregates, Inc. pit number 7, Loxahatchee, Palm Beach County, Florida. [26°42.20′ N, 80°20.97′ W] At 15 m depth. Holey Land Member of the Bermont Formation. Aftonian Pleistocene (~1.6 million years before present).

fossil molluscan faunas of Florida and the tropical western Atlantic.

Remarks: The large size, conical shell shape, presence of multiple, fine, axial ribs and a simple, flared lip serve to distinguish *Cerion petuchi* new species from all fossil cerionids reported from the Late Oligocene / early Miocene silex beds of Ballast Point, Florida. *Cerion* (*Microcerion*) *floridanum* Dall, 1915 had a much smaller shell with smoothly rounded whorls and a distinctive, extremely broad, concavely rounded outer lip. Both *Cerion* (*Eostrophia*) *anodonta* Dall, 1890 and *Cerion* (*Eostrophia*) *anodonta* var. *floridanum* Dall, 1915 had shells that are cylindrical in shape, with a smooth surface and smaller, rounder apertures. Pilsbry (1946: 161) reported a single fossil specimen that he identified as *Cerion incanum* from Clewiston, Florida, from the younger Fort Thompson Formation (Pleistocene). This specimen, originally in the McGinty collection, was not illustrated and could not be located.

Of the Recent *Cerion* inhabiting the Florida Keys, *Cerion petuchi* new species most closely resembles *Cerion incanum saccharimeta* Pilsbry and Vanatta, 1899, which is also characterized by its large size and conical shell shape, but differs in having coarser and more irregularly spaced axial sculpture, a rounder aperture and a simpler, less flared outer lip. *Cerion petuchi* new species most closely resembles *Cerion agassizii* Dall, 1894, from the Pleistocene (ca. 120,000 years BP) dunes of New Providence Island (Bahamas), a species that is readily distinguished on the basis of having fewer, more irregularly spaced axial ribs, more pronounced parietal and



Figures 10–11. *Cerion petuchi* new species. **10.** Apical view of protoconch of holotype. **11.** Details of apertural dentition of holotype.

columellar teeth, and a "duplex" outer lip, which forms a concavely rounded, bow-like structure most pronounced along the anterior margin of the aperture. *Cerion picturata* (Maynard and Clapp *in* Maynard, 1921) from Pleistocene/Holocene deposits on Cabbage Key in the Berry Islands (Bahamas) is also similar. It lacks the "duplex" outer lip, but differing in having coarser, more axially aligned sculpture. A similar phenotype survives in the Recent fauna of Guana Key, Berry Islands as *Cerion arbusta* (Maynard and Clapp *in* Maynard, 1919).

GEOGRAPHIC AND TEMPORAL DIVERSITY OF THE CERIONIDAE

Data on geographic distribution and geologic age for the 600 species level taxa within the family Cerionidae were compiled based primarily on information from the *Cerion* website (Harasewych, 2009). Taxa were assigned to islands or island groups based on their type localities. Objective synonyms and *nomina nuda* were excluded, as were taxa with unknown [e.g., *Cerion cumingiana* (Pfeiffer, 1852)] or clearly erroneous type localities [e.g., *Cerion antonii* (Küster, 1847) from British Guiana], but subjective synonyms were generally counted as separate taxa. Results are shown in Table 1.

Several authors have noted the multitude of taxonomic names applied to the abundant phenotypes within the Cerionidae and speculated that the actual number of valid species may be on the order of 1–20% of the number of names now extant (e.g., Clench, 1957; Woodruff, 1978). Although the numbers of taxa appearing in Table 1 will inevitably be revised downward based on detailed systematic studies, certain patterns are striking and will likely persevere. Most conspicuous is the observation that by far the greatest diversity of Cerionidae occurs on the Great Bahama Bank (47.2%, of all named Recent species level taxa), while the fauna of Cuba comprises 32.8% of all Recent species level diversity. Both these areas have alternated between being large, contiguous land masses and archipelagos during the glacial and interglacial sea-level fluctuations of the Pleistocene and Holocene. Iturralde-Vinent (2006:figs.7,8,10,11) has shown that Cuba consisted of a series of isolated islands from the Oligocene to the Late Pleistocene, with the present shape of the island attained 8,000–6,000 years ago.

By contrast, the combined fauna of the southeastern Bahamian Islands and the Turks and Caicos Islands, which would have remained isolated during the lowest sea levels, comprises only 9.3% of total Recent cerionid diversity. None of the remaining regions populated by cerionids contribute more than 3.5% of the Recent diversity.

This pattern is even more pronounced during the Pleistocene / Holocene, when the Great Bahama Bank accounted for 90.0% of the 50 described species level taxa. The isolated southeastern Bahamian Islands collectively accounted for 4.0% of the named fauna, with only single species (2.0% of the fauna) reported from Cuba, Florida and the western Virgin Islands. Prior to the Pleistocene, the fossil record is exceedingly sparse, with only three taxa reported from the Oligocene, three from the Paleocene, and one from the Cretaceous.

A ZOOGEOGRAPHIC HYPOTHESIS FOR CERIONIDAE

The early fossil record of the Cerionidae consists of few taxa represented by rare specimens that nevertheless provide insights into the zoogeographic history of the family. The earliest record for the family (*Cerion acherontis* Roth and Hartmann, 1998) is based on a single, damaged specimen from the Late Cretaceous of Montana. The genus *Brasilennea*, represented by three species from the Paleocene of Itaboraí Basin, Brazil, (Salvador et al., 2011; Salvador and Simone, 2012) has

recently been transferred from the family Streptaxidae to the Cerionidae. Western Laurasia (North America) and western Gondwana (South America) were separated by a marine waterway during the Jurassic (Callovian), with land bridges developing during the Late Cretaceous (Campanian / Maastrichtian) (75–65 Ma) via a proto-Antillean island arc, and again during the Plio-Pleistocene (2.5 Ma) via the Panama land bridge (Iturralde-Vinent, 2006). Parodiz (1969: 189, Map 7) noted that many of the families of South American non-marine mollusks are of Nearctic origin, having migrated to South America at the close of the Cretaceous. Given the presence of cerionids in South America during the Paleocene, it is probable that members of this family were part of this Late Cretaceous migration.

The recent description of the genus *Mexistrophia* from cool, coniferous forests in the highlands of central Mexico (Thompson, 2012), suggests that this genus was an early offshoot that diverged during the Late Cretaceous, prior to the adaptations to near shore, halophilic habitats of most living cerionids.

Uit de Weerd (2008: 323, fig. 8) explored a vicariance model in which the proto-Antillean island arc may have carried North American lineages, including Cerionidae and Urocoptidae, northeastward during the early Tertiary until it collided with the Bahamas platform during the Middle Eocene (Pindell, 1994). However, Iturralde-Vinent (2006) noted that it was not until the Middle Eocene that permanent lands, required for the development of a terrestrial fauna, were present within the Caribbean realm. An alternative hypothesis, that a mid-Cenozoic GAARlandia (GAAR = Greater Antilles + Aves Ridge) land bridge provided the means for colonization of the Greater Antilles from northwestern South America (see Iturralde-Vinent, 2006: fig. 6) during a 1–2 Myr interval at the Eocene-Oligocene boundary has been proposed (Iturralde-Vinent and MacPhee, 1999, see Ali, 2012 for a review). Iturralde-Vinent (2006: fig. 13) provided a detailed account of the patterns and chronology of interconnections among the various land masses within the Caribbean. This model is applied to produce a zoogeographic hypothesis for the distribution of Cerionidae since the Cretaceous (Figure 12), and is concordant with the absence of cerionids in Jamaica and the Lesser Antilles.

As there was never a land connection between Cuba and the Bahamas, the Great Bahamas Bank must have been populated initially by propagules from Cuba or the Cuban archipelago dispersed by hurricanes, with the Little Bahama Bank colonized by propagules from the Great Bahama Bank. The role of hurricanes in dispersing propagules of *Cerion* among neighboring islands has been accepted as stochastic events with a major influence on biogeographic patterns of cerionids (e.g., Pilsbry, 1907; Mayr and Rosen, 1956; Clench, 1957). Like Cuba, the islands of the Little and Great Bahama Banks were sequentially conjoined and separated by changes in sea level resulting in multiple instances of secondary contact between populations isolated during interglacial high

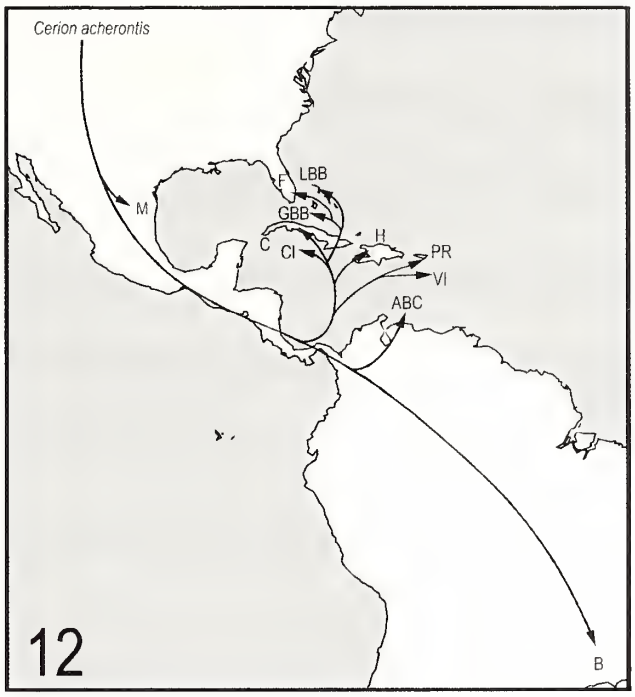


Figure 12. Hypothesized zoogeographic history of the family Cerionidae based on the age and distribution of fossil and Recent Taxa (Table 1) and paleogeographic reconstructions of the Caribbean region from the Cretaceous to Recent (Iturralde-Vinent, 2006). **ABC,** Aruba, Bonaire and Curaçao; **B,** *Brasilennea*; **C,** Cuba; **CI,** Cayman Islands; **F,** Florida; **GBB,** Creat Bahama Bank; **H,** Hispaniola; **LBB,** Little Bahama Bank; **M,** *Mexistrophia*; **PR,** Puerto Rico; **VI,** western Virgin Islands

stands. Thus, populations that were isolated on small, individual islands during interglacial periods were able to expand their ranges and interbreed during glacial periods.

The islands of the Turks and Caicos and many of the southeastern Bahamian islands never had direct connection with the Bahama Banks or Cuba, and remained isolated by deep channels even during glacial sea level minima. The cerionid faunas of these islands are thus the summation of hurricane-born propagules reaching their shores from Cuba, Hispaniola, and the Bahamian Banks and islands.

The Cayman Islands were joined to southeastern Cuba by shallow banks during the Pliocene and are likely to have been colonized by cerionids from this region.

Early authors (e.g., Binney, 1851; Pilsbry, 1902, 1907, 1946; Dall, 1905) considered the living *Cerion* of the Florida Keys to be derived from populations of northern Cuba. However, a molecular phylogeny based on partial sequences of the cytochrome c oxidase I gene (Harasewych et al. 2011:fig. 16) shows them to be most closely related to samples from Andros Island on the Great Bahama Bank. The occurrence of *Cerion petuchi* new species in the Pleistocene of southeastern Florida is consistent with a Bahamian origin for the cerionid fauna of the Florida Keys. However, the origin and

relationships of the upper Oligocene–lower Miocene cerionids of the central west coast of Florida are enigmatic. There was never a direct connection between GAARlandia and Florida, although this large peninsula altered current patterns that might have facilitated rafting of a propagule from the northern portions of GAARlandia or one of its subsequent archipelagos to the west coast of Florida (Iturralde-Vinent, 2006: fig. 12). Alternatively, a separate offshoot of the Late Cretaceous *Cerion acherontis* may have extended eastward along the northern shores of the Gulf of Mexico, reaching the coast of central western Florida by the late Oligocene. These are, at best, speculative scenarios for the origin of a cerionid fauna that does not appear to be ancestral to the Pleistocene or Recent *Cerion* of southeastern Florida.

The zoogeographic hypothesis depicted in Figure 12 was converted to a phylogenetic tree (Figure 13), with dates attributed to several nodes based on Iturralde-Vinent (2006: figs. 10, 13). Dashed lines represent faunas for which molecular data is lacking. The solid lines represent branches that are supported by a molecular phylogeny of Cerionidae based on amino acid sequences of a portion of the mitochondrial COI gene (Harasewych et al., 2011: fig. 17).

The early history of the Cerionidae was determined by overland dispersal and vicariance caused by tectonic events. *Mexistrophia* was isolated from the South American cerionids since the Upper Cretaceous by the formation of a seaway brought about by the displacement of the proto-Antillean island arc by the eastward movement of the Caribbean Tectonic Plate from the eastern Pacific. *Cerion sensu stricto*, which inhabits the islands of Aruba, Curaçao and Bonaire, was isolated from the remaining Caribbean lineages of *Cerion* by the break-up of GAARlandia and continued displacement of the Antillean blocks and terranes northeastward by the advancement of the Caribbean Tectonic Plate. The opening of the Mona Passage during the lower Miocene separated the terrestrial faunas of Cuba and Hispaniola from those of Puerto Rico and the Virgin Islands. Hispaniola was separated from eastern Cuba during the mid to late Miocene, while the Virgin Islands and Puerto Rico were last joined during the Pliocene (Iturralde-Vinent 2006: fig. 13). With the exception of Cuba, the *Cerion* faunas of these islands are not diverse.

The absence of a land connection between the islands of the Bahamas (or the Turks and Caicos Islands) and the Greater Antilles precluded overland colonization. Rather, these islands must have initially been populated by small propagules dispersed from the Greater Antilles either by rafting or carried by hurricanes. Over time, *Cerion* likely reached the more remote islands of the Bahamas and Florida by a stepping stone pattern. It is interesting to note that Bartsch's introductions of *Cerion* into the Florida Keys generally consisted of large numbers of individuals (n=500) and the resulting colonies remained unchanged for multiple generations (see Bartsch [1920] for a summary). However, experimental

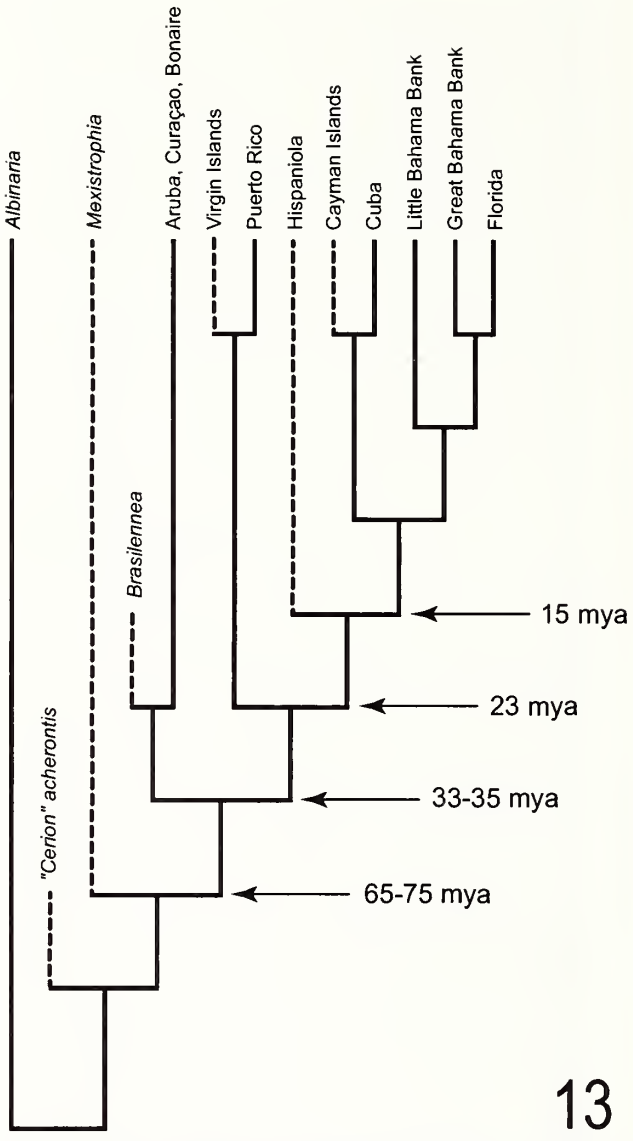


Figure 13. Phylogenetic relationships among living and fossil cerionid faunas derived from phylogeographic hypothesis in Figure 12. Solid lines represent portions of tree that are concordant with a molecular phylogeny of Cerionidae based on amino acid sequences of a portion of the mitochondrial COI gene (Harasewych et al., 2011:fig. 17). Dashed lines represent faunas for which molecular data is lacking. Dates attributed to nodes are from Iturralde-Vinent (2006: figs. 10, 13).

introductions of *Anolis* lizards within the Bahamas using much smaller propagules (5 or 10 individuals) resulted in rapid differentiation over a 10–14 year period (Losos et al. 1997).

Sea-level fluctuations caused by Pleistocene and Holocene glacial / interglacial cycles altered the geography and faunal diversity of individual islands to varying degrees. During interglacial periods, terrestrial faunas would be confined to isolated refugia on hill tops and mountains that remained above the elevated sea-levels. Drops in sea level during glacial periods would join the

islands of such archipelagos into larger platforms permitting previously isolated populations to expand their ranges and come into contact. Thus, such sea-level changes amplified diversity by repeatedly isolating and recombining / hybridizing neighboring populations of islands and banks defined during glacial periods.

The degree to which the diversity of a particular bank or island was amplified during a glacial cycle varied significantly, being a function of the number of islands that were united during glacial periods. The diversity of distinctive cerionid phenotypes (hybrids) on the Great Bahama Bank would have been greatly amplified by multiple cycles of glaciation due to the high number of islands that were isolated and conjoined. By contrast, the diversity of isolated islands such as San Salvador in the Bahamas, which remained isolated throughout the glacial cycles, would have changed little.

This ability of *Cerion* to hybridize, producing distinctive phenotypes and alozymes not present in either parent population, have contributed to the proliferation of taxonomic names, especially during the late 19th and early 20th centuries. Subsequent genetic and morphometric studies have shown that such novel phenotypes are often ephemeral, surviving on the order centuries (Woodruff and Gould, 1987) to millennia (Goodfriend and Gould, 1996). Further, all documented instances of hybridization have been between geographically and probably also phylogenetically proximal taxa [e.g., Hybrid on Bahia Honda Key, Florida = *Cerion incanum* (Florida) + *Cerion cassablancae* (Andros Island, Bahamas); Hybrid on Newfound Harbor Key, Florida= *Cerion incanum* (Florida) + *Cerion viaregis* (Andros Island, Bahamas); *Cerion tridentata costellata* Fort Jefferson, Garden Key, Dry Tortugas, Florida = hybrid of *Cerion tridentata* (Rincon de Guanabon, Cuba) + *Cerion sculptum* (Mariel, Cuba); Fossil hybrid on Great Inagua = *Cerion excelsior* (Great Inagua) + *Cerion rubicundum* (unspecified, but presumably a nearby island)]. None of Bartsch's experimental attempts to hybridize *Cerion* from Curaçao, Puerto Rico or Cuba with each other, or with *Cerion* from Florida or the Bahamas were successful.

ACKNOWLEDGMENTS

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LITERATURE CITED

Ali, J.R. 2012. Colonizing the Caribbean: is the GAARlandia land-bridge hypothesis gaining a foothold? Journal of Biogeography 39: 431–433.

Baker, H.B. 1924. Land and freshwater molluscs of the Dutch Leeward Islands. Occasional Papers, Museum of Zoology, University of Michigan, No. 152, 158 pp., 21 pls.

Bartsch, P. 1920. Experiments in the breeding of Cerions. Papers of the Department of Marine Biology, Carnegie Institution of Washington, 14 (282): 1–54, pls. 1–59.

Binney, A. 1851. The Terrestrial Air-Breathing Mollusks of the United States, and the Adjacent Territories of North America: Described and Illustated by Amos Binney. (Edited by Augustus A. Gould). Volume 1: 1–266, pls. 1–16.

Clench, W.J. 1957. A catalog of the Cerionidae (Mollusca: Pulmonata). Bulletin of the Museum of Comparative Zoology 116: 121–169.

Clench, W.J. 1961. Land and Freshwater Mollusca of Caicos, Turks, Ragged Islands and Islands on the Cay Sal Bank, Bahamas. Occasional Papers on Mollusks MCZ Harvard, 2(26): 229–259, pls. 40–43.

Dall, W.H. 1905. Fossils of the Bahama Islands, with a list of the non-marine mollusks. In: Shattuck, G.B. (Ed.) The Bahama Islands. The Geographical Society of Baltimore, Baltimore, pp. 23–47, pls. 10–13.

Goodfriend, G.A., and S.J. Gould. 1996. Paleontology and chronology of two evolutionary transitions by hybridization in the Bahamian land snail *Cerion*. Science 274: 1894–1897.

Gould, S.J. 1984. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curaçao: a way of studying nonadaptation. Systematic Zoology 33: 217–237.

Gould, S.J. and C. Paull. 1977. Natural History of *Cerion* VII: Geographic variation of *Cerion* (Mollusca: Pulmonata) from the eastern end of its range (Hispanola to the Virgin Islands): coherent patterns and taxonomic simplification. Breviora 445: 1–24.

Harasewych, M.G. 2009. *Cerion*: a web-based resource for *Cerion* research and identification. [WWW database (version 1.02)] URL http://invertebrates.si.edu/Cerion/

Harasewych, M.G., M. Sikaroodi, and P.M. Gillevet, 2011. The Delray Beach, Florida colony of *Cerion* (*Paracerion*) *tridentatum costellata* Pilsbry, 1946 (Gastropoda: Pulmonata: Cerionidae): Evidence for indirect Cuban origins. The Nautilus 125:173–181.

Harasewych, M.G. and J. Strauss. 2006. A new record of introduced *Cerion* (Gastropoda: Pulmonata: Cerionidae) in southeastern Florida. The Nautilus 120: 94–100.

Hearty, P.J., Kaufman, D.S. 2009. A *Cerion*-based chronostratigraphy and age model from the central Bahama Islands: Amino acid racemization and ^{14}C in land snails and sediments. Quaternary Geochronology 4: 148–159.

Iturralde-Vinent, M.A. 2006. Meso-Cenozoic Caribbean paleogeography: implications for the historical biogeography of the region. *International Geology Review* 48: 791–827.

Iturralde-Vinent, M.A. and R.D.E. MacPhee. 1999. Paleogeography of the Caribbean region: implications for Cenozoic biogeography. Bulletin of the American Museum of Natural History 238: 1–95.

Losos, J.B., K.I. Warheit, and T.W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 387: 70–73.

Maynard, C.J. 1889–1896. Monograph of the Genus *Strophia*, A Group of Tropical and Sub-tropical Land Shells. Contribution to Science (1889–1890) 1:ii+204(+2), pls.1–6,8–15; (1893–1894) 2:1–204, pls. 1,2,4–12; (1896) 3:1–48, pls. 1–7. privately published, Newtonville, MA.

Mayr, E., and C.B. Rosen. 1956. Geographic variation and hybridiation in populations of Bahama snails (*Cerion*). American Museum of Natural History Novitates 1806: 1–48.

Parodiz, J.J. 1969. The Tertiary Non-marine Mollusca of South America. Annals of the Carnegie Museum 40: 1–242.

Petuch, E.J. 2003. Cenozoic seas: the view from eastern North America. CRC Press, Boca Raton, London, and New York, 308 pp.

Petuch, E.J. and C.E. Roberts. 2007. The Geology of the Everglades and Adjacent Areas. CRC Press, Boca Raton, London, and New York. 212 pp.

Pilsbry, H.A. 1901–1902. Family Cerionidae. Manual of Conchology. Ser. 2. Pulmonata. Academy of Natural Sciences of Philadelphia. (1901) 14(53–55): 1–192, pls. 1–26; (1902) 14(56): 193–286, pls. 27–47.

Pilsbry, H.A. 1907. Origin of the Tropical Forms of the Land Molluscan Fauna of Southern Florida. Proceedings of the Academy of Natural Sciences of Philadelphia 59: 193.

Pilsbry, H.A. 1946. Land Mollusca of North America. The Academy of Natural Sciences of Philadelphia, Monograph3, Volume 2, part 1: viii + 520 pp.

Pindell, J. 1994. Evolution of the Gulf of Mexico and Caribbean. In: Donovan, S.K., T.A. Jackson, T.A. (eds.) Caribbean geology, an introduction. University of West Indies Publishers Association, Kingston, pp. 13–40.

Roth, B. and J.H. Hartman. 1998. A probable *Cerion* (Gastropoda: Pulmonata) from the uppermost Cretaceous Hell Creek Formation, Garfield County, Montana. Paleobios 18(2–3): 16–20.

Salvador, R.B., B. Rowson, and L.R.L. Simone. 2011. Rewriting the fossil history of Cerionidae (Gastropoda: Pulmonata): new family assignment of the Brazilian Paleocene genus *Brasilennea* Maury, 1935. Journal of Molluscan Studies 77: 445–447.

Salvador, R.B. and L.R.L. de Simone. 2012. New fossil pulmonate snails from the Paleocene of Itaborai Basin, Brazil (Pulmonata Cerionidae Strophocheilidae, Orthalicidae). Archiv für Molluskenkunde 141: 43–50.

Thompson, F.G. 2011. *Mexistrophia*, a new genus of Cerionidae from Mexico (Gastropoda: Pulmonata: Urocoptoidea). The Nautilus 125(4):182–192.

Uit de Weerd, D.R. 2008. Delimitation and phylogenetics of the diverse land-snail family Urocoptidae (Gastropoda: Pulmonata) based on 28S rRNA sequence data: a reunion with *Cerion*. Journal of Molluscan Studies 74: 317–329.

Woodruff, D.S. 1978. Evolution and adaptive radiation of *Cerion*: a remarkably diverse group of West Indian land snails. Malacologia 17: 223–239.

Woodruff, D.S. and S.J. Gould. 1987. Fifty years of interspecific hybridization: genetics and morphometrics of a controlled experiment on the land snail *Cerion* in the Florida Keys. Evolution 41: 1022–1045.

A new species of *Fusivoluta* Martens, 1902 (Gastropoda: Volutidae) from Mozambique

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ABSTRACT

During a recent expedition to Mozambique, several specimens attributed to the genus *Fusivoluta* von Martens, 1902 were collected between 1100 and 1820 m deep. Among them, a new species has been found and is here described and compared with the other East African *Fusivoluta*. Several live-collected specimens, belonging to the newly described species and to *Fusivoluta clarkei* Rehder, 1969 were sequenced for a nuclear gene (28S), revealing fixed differences between the two species.

Additional keywords: Molecular taxonomy, 28S gene, *Fusivoluta profundorum* nov. sp., Gastropoda, Mozambique, Volutidae

INTRODUCTION

The MAINBAZA expedition took place in April 2009 on board R/V Vizconde de Eza, a research vessel from the Secretaria del Mar of the Spanish Ministerio de Medio Ambiente, Medio Rural y Marino, as part of a joint project between Muséum National d'Histoire Naturelle (MNHN) and Instituto Español de Oceanografia (IOE). Forty-six hauls were conducted at depths between 100 and 1820 meters on four transects off Maputo, Inhambane, Bazaruto, and the mouth of the Zambezi River. The expedition discovered many new species of benthic invertebrates, several of which have already been named (Alf et al., 2010; Cabezas et al., 2010; Komai and Chan, 2010; Richer de Forges, 2010). Among them, a new bathyal Volutidae has been identified, and is described as new in this article. Morphological differences clearly separate it from other *Fusivoluta* species. Additionally, several live-collected specimens of this new species and of *F. clarkei* were sequenced for the 28S gene to molecularly confirm the validity of the two species.

MATERIALS AND METHODS

Study Material: The studied material identified as *Fusivoluta* spp. was collected in six different stations (details are provided below) during the Mainbaza expedition. Three of them (CP3139, CP3141, and CP3154) provided live material (five specimens in total) that was used for molecular analyses (Table 1). Two of them were morphologically identified as *Fusivoluta clarkei*; the three others were assigned to the new species. All vouchers are deposited in the MNHN; specimen data are also recorded in BOLD and sequences are published in GenBank (accession numbers are given in Table 1). Another species, *Athleta mozambicana* (Rehder, 1972), also belonging to the family Volutidae, was collected during the same expedition; it was added to the analysis as closely related outgroup. Two other Volutidae species were available in GenBank (*Amoria hunteri* – accession number DQ916584.1 and *Alcithoe aillaudorum* – accession number GU440153.1). A distant outgroup belonging to the family Muricidae was used to artificially root the phylogenetic tree (*Chicoreus subpalmatus*, accession number GU440174.1).

DNA Analysis: Live-collected specimens were preserved in alcohol and their DNA was extracted following the same protocol as in Puillandre et al. (2011). A fragment of the 28S gene was amplified using the primer C1′ (ACC CGC TGA ATT TAA GCA T) and D2 (TCC GTG TTT CAA GAC GGG) (Jovelin and Justine 2001). PCR reactions were performed in 25 µL final volume, containing approximately 3 ng template DNA, 1.5 mM MgCl2, 0.26 mM of each nucleotide, 0.3 µM of each primer, 5% DMSO and 0.75 U of Taq Polymerase (Qbiogene). Amplification products were generated by an initial denaturation step of 5 min at 94 °C followed by 35 cycles at 94 °C for 40 s, annealing at 52°C and by an extension at 72°C for 1 min. The final extension was at 72°C for 5 min. PCR products were purified and sequenced by a sequencing facility (Eurofins). All genes were sequenced in both directions for increased accuracy. Sequences were manually aligned, and phylogenetic analyses were performed using the bayesian approach implemented in MrBayes (Huelsenbeck et al. 2001). Two parallel analyses were run, consisting each of

Table 1. List of specimens used for the phylogenetic analysis

MNHN Number	Family	Genus	Species	Station	BOLD ID	GenBank number
IM-2009-7340	Volutidae	*Fusivoluta*	*clarkei*	CP3141	NEOGA1168-12	JQ775166
IM-2009-7392	Volutidae	*Fusivoluta*	*profundorum*	CP3139	NEOGA1170-12	JQ775169
IM-2009-9488	Volutidae	*Fusivoluta*	*profundorum*	CP3139	NEOGA1166-12	JQ775167
IM-2009-9489	Volutidae	*Fusivoluta*	*profundorum*	CP3139	NEOGA1165-12	JQ775168
IM-2009-9495	Volutidae	*Fusivoluta*	*clarkei*	CC3154	NEOGA1169-12	JQ775165
IM-2009-9487	Volutidae	*Athleta*	*mozambicana*	CP3146	NEOGA1167-12	JQ775164
	Volutidae	*Amoria*	*hunteri*			DQ916584.1
	Volutidae	*Alcithoe*	*aillaudorum*			GU440153.1
	Muricidae	*Chicoreus*	*subpalmatus*			GU440174.1

eight Markov chains of 5,000,000 generations. All other parameters were set to default.

Abbreviations: DNMH: Delaware Museum of Natural History, Greenville, Delaware; MNHN: Muséum National d'Histoire Naturelle, Paris; RSA: Republic of South Africa; Stn: station.

RESULTS

Phylogenetic Analysis: The phylogenetic tree (Figure 1) clearly shows that all the specimens identified as *Fusivoluta* belong to a single well-supported clade (Posterior Probability PP = 1). Within this clade, two reciprocally monophyletic groups are defined, one corresponding

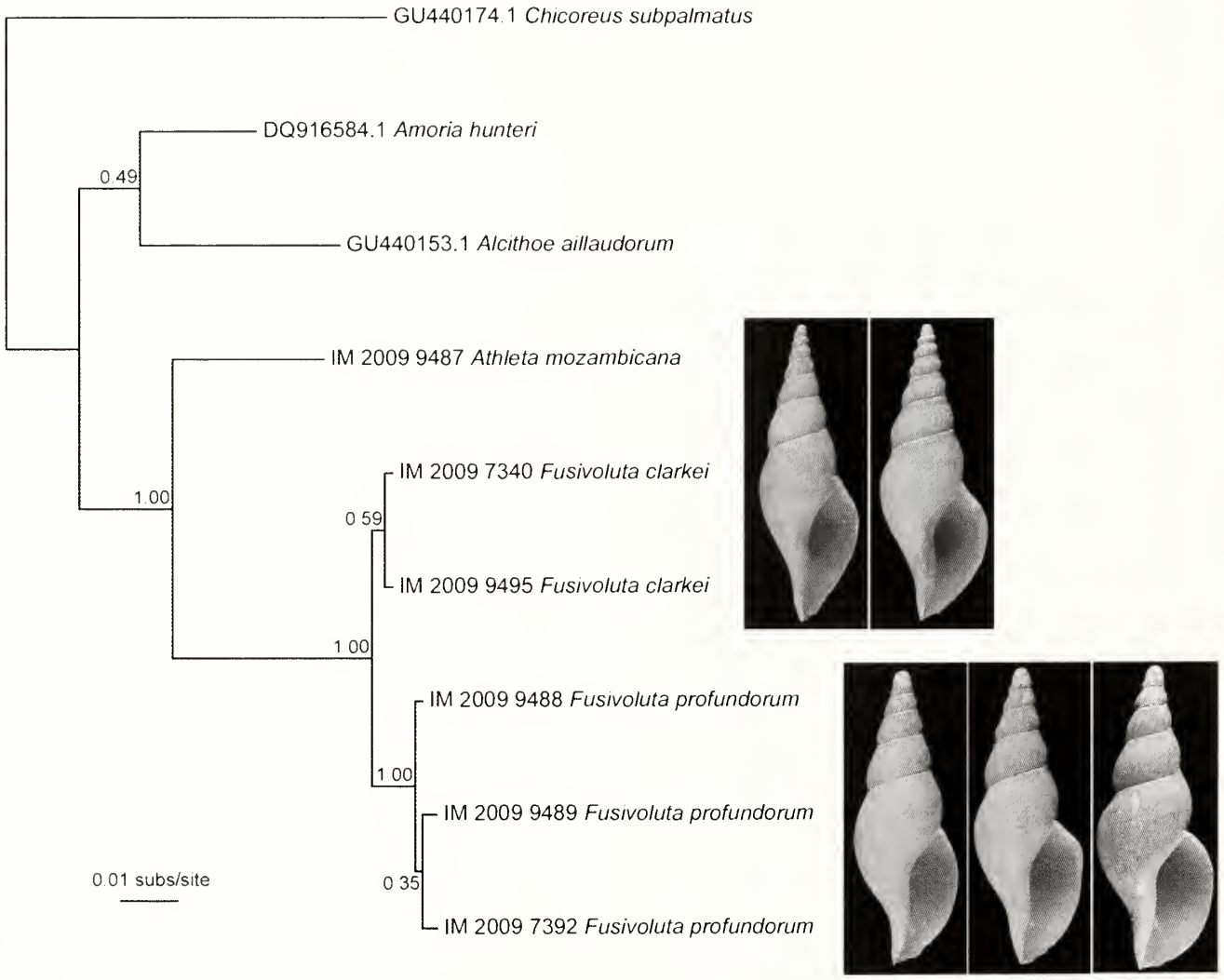

Figure 1. Phylogenetic tree.

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                461
IM_2009-7340 GGGCAGGAGA TCTTCAACGA --CTCTCCCG GCGC-GGGGA CGCGTGCCGG
IM_2009-9495 GGGCAGGAGA TCTTCAACGA --CTCTCCCG GCGC-GGGGA CGCGTGCCGG
IM_2009-9489 GGGCAGGAGA TCTTCAACGA GACTCTCCCG GCGCTGGGGA CGCGTGCCGG
IM_2009-7392 GGGCAGGAGA TCTTCAACGA GACTCTCCCG GCGCTGGGGA CGCGTGCCGG
IM_2009-9488 GGGCAGGAGA TCTTCAACGA GACTCTCCCG GCGCTGGGGA CGCGTGCCGG
                511
                CCGTGTGCAC TTTCCGCGGG CAGAGCGCCA CGACCGGTTC TTGGGCGGTC
                CCGTGTGCAC TTTCCGCGGG CAGAGCGCCA CGACCGGTTC TTGGGCGGTC
                CCGTGTGCAC TTTCCGCGGG CAGAGCGCCA CGACCGGTTC TTGGGCGGTC
                CCGTGTGCAC TTTCCGCGGG CAGAGCGCCA CGACCGGTTC TTGGGCGGTC
                CCGTGTGCAC TTTCCGCGGG CAGAGCGCCA CGACCGGTTC TTGGGCGGTC
                561
                AGAAGCTGGC -GAGGATGGT AGGCGCGC-G TCTCCGCGCG TGCGCTGGTA
                AGAAGCTGGC -GAGGATGGT AGGCGCGC-G TCTCCGCGCG TGCGCTGGTA
                AGAAGCCGGC -GAGGATGGT AGGCGCGTTG TCTCCGCACG TGCGCTGGTA
                AGAAGCCGGC -GAGGATGGT AGGTGCGTTG TCTCCGCACG TGCGCTGGTA
                AGAAGCCGGC -GAGGATGGT AGGCGCGTTG TCTCCGCACG TGCGCTGGTA
                611
                CAGCCTC-GC CTGTCCCGAT CCGCCC-GGG GACCGAGGAG CCGCCGCCGG
                CAGCCTC-GC CTGTCCCGAT CCGCCC-GGG GACCGAGGAG CCGCCGCCGG
                CAGCCTC-GC CTGTCCCGAT CCGCCC-GGG GACCGAGGAG CCGCCGCTGG
                CAGCCTC-GC CTGTCCCGAT CCGCCC-GGG GACCGAGGAG CCGCCGCTGG
                CAGCCTC-GC CTGTCCCGAT CCGCCC-GGG GACCGAGGAG CCGCCGCTGG
                661
                T-G-TAGGCC GCCCC-GCCC TCCTGGGATG TTCGACTGGC AGAGACTGGG
                T-G-TAGGCC GCCCC-GCCC TCCTGGGATG TTCGACTGGC AGAGACTGGG
                T-G-TAGGCC GCCCCCGCCC TCCTGGGATG TTCGACTGGC AGAGACTGGG
                T-G-TAGGCC GCCCCCGCCC TCCTGGGATG TTCGACTGGC AGAGACTGGG
                T-G-TAGGCC GCCCCCGCCC TCCTGGGATG TTCGACTGGC AGAGACTGGG
                711
                CAACCGTGTC TGCTGACCGC TTCCTTGGAC GGCAAAAACC AAGGGC---T
                CAACCGTGTC TGCTGACCGC TTCCTTGGAC GGCAAAAACC AAGGGC---T
                CAACCGTGTC TGCTGACCGC TTCCTTGGAC GGCAAAAACC AAGGGCGTGT
                CAACCGTGTC TGCTGACCGC TTCCTTGGAC GGCAAAAACC AAGGGCGTGT
                CAACCGTGTC TGCTGACCGC TTCCTTGGAC GGCAAAAACC AAGGGCGTGT
                761
                GGGCCC--GC CGGCACAGGG TCGGTGGCGA ATCGGTCGGC CCTCCACCTG
                GGGCCC--GC CGGCACAGGG TCGGTGGCGA ATCGGTCGGC CCTCCACCTG
                GGGCCT--GC CGGCACAGGG TCGGTGGCGA ATCGGTCGGC CCTCCACCTG
                GGGCCT--GC CGGCACAGGG TCGGTGGCGA ATCGGTCGGC CCTCCACCTG
                GGGCCT--GC CGGCACAGGG TCGGTGGCGA ATCGGTCGGC CCTCCACCTG
```

Figure 2. 28S alignment of the two specimens of *Fusivoluta clarkei* (above) and three specimens of *F. profundorum* (below) showing the diagnostic characters that discriminate the two species.

to *Fusivoluta clarkei*, with low statistical support (Posterior Probability PP = 0.59), the second to *Fusivoluta profundorum* with a high statistical support (PP = 1). Furthermore, the analysis of the 28S alignment reveals the existence of several fixed mutations and insertions (10 in total, shown on figure 2) that distinguish the two species. These results thus confirm the morphological identifications and support the validity of the two species.

In this partial tree, the relative closeness of *Fusivoluta* to *Athleta* is noticeable. Nevertheless, no conclusion must be drawn yet, pending the construction of a complete phylogenetic tree of the Volutidae.

SYSTEMATICS

Family Volutidae Rafinesque, 1815
Subfamily Calliotectinae Pilsbry and Olsson, 1954.

Genus ***Fusivoluta*** **Von Martens, 1904.**

Type Species: *Fusivoluta anomala* von Martens, 1902

Fusivoluta profundorum **new species** (Figures 3–21)

Diagnosis: Shell of moderate size, fusiform, with high spire. Protoconch bulbous, with 2–3 whorls. Teleoconch sculptured with axial ribs. Columella without plaits. Aperture with flared outer lip when adult. Fasciole indistinct. Siphonal notch absent. Thin periostracum and horny operculum present.

Description: Adult shell of moderate size for genus (length 45–55 mm), light, fusiform. Surface dull covered by thin, adherent, gray periostracum. Protoconch small (average width: 2 mm), with 2 whorls, first whorl flattened, subsequent very convex. Transition protoconch–teleoconch sharp. Spire moderately high, forming average of 48% of total length of shell. Protoconch and abapical part of spire usually eroded. Teleoconch of 5 whorls, last slightly inflated. Suture indented. Sculpture of axial ribs (14–15 on antepenultimate whorl), blunt or knobbed on some specimens, prominent onto spire, then becoming obsolete on half abapical part of penultimate whorl and on whole last whorl. Spiral sculpture of numerous, regularly spaced, minute cords covering whole teleoconch, becoming weaker on last whorl, crossed by faint axial lirae giving cancellate appearance (Figure 40, left). Aperture large, semi-circular, with outer lip thin and anteriorly flared. Columella slightly sigmoid without plaits. Anterior canal very short without siphonal notch. Surface of teleoconch and aperture gray-white, anterior part of columella and inner edge of outer lip slightly tinged with orange.

Type Material: Holotype MNHN 22816 (=IM-2009-7392), 49.0×18.5 mm (Figures 3–5); paratype I, IM-2009-9489, Stn CP3139, 1195 m, 45.7×17.5 mm (Figures 6–7); paratype II IM-2009-9488, Stn CP3139, 1195 m, 44.6×16.3 mm (Figures 8–9); paratype III, stn CC3158, 1220–1248 m, 43.3×17.7 mm (Figures 10–11).

Other Material Examined: Station CP3139, 23°35′ S, 36°06′ E, 1100–1200m, 8 specimens: 49.5×17.4 mm, 48.0×17.8 mm, 48.0×17.3 mm, 47.2×18.2 mm, 44.5×19.8 mm, 42.9×18.3 mm, 42.7.0×16.0 mm, 43.0×17.2 mm. Station CC3158, 21°46′ S, 36°12′ E, 1220–1248 m, 2 specimens: 43.3×17.6 mm (live), 39.6×16.7 mm. Station CC3156, 21°40′ S, 36°35′ E, 1810–1820 m, 1 specimen: 56.3×21.3 mm. Station CP3145, 21°47′ S, 36°24′ E, 1408–1421 m, 2 specimens: 55.5×40.0 mm, 50.8×18.0 mm.

Type Locality: 23°35′ S, 36°06′ E, 1100–1200 m, station CP3139.

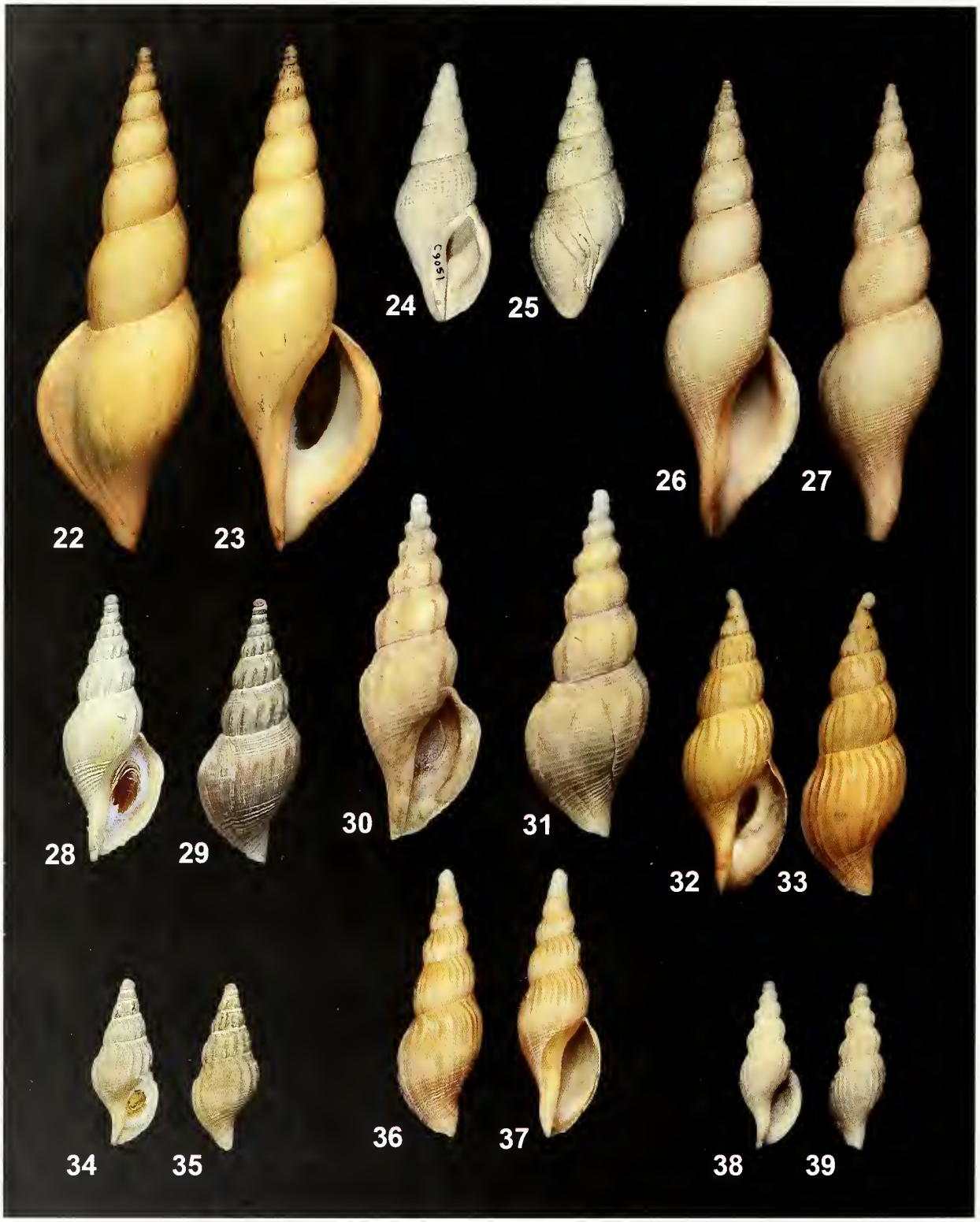
Etymology: Specific epithet refers to the deep-sea habitat of the new species.

Distribution: Endemic in waters off Mozambique. A distribution between latitudes 21–23° S, in 1100–1500 m deep is revealed by the trawling operations, but the southern and northern limits are still imprecise because of lack of exploration beyond the explored range (see map, Figure 48).

Table 2. Summary of conchological differences between the five comparable *Fusivoluta*.

	profundorum	*clarkei*	*barnardi*	*decussata*	aff. *anomala*	*anomala*
Protoconch	bulbous, 2 whorls, the first flattened	rounded, 1.5 whorl, the first immersed	raised, bulbous, 1.25 whorl	mamillate of 1.5 whorl	turreted, of 2 very convex whorl	raised, 1.5 whorl, the first flattened
axial ribs	14–15 often knobbed	19–20 moderately angulate	22–23 very faint	absent	14–15 slightly angulate	12–13 strongly angulate
sculpture of last whorl	cancellate, no knobs	dominant spiral threads, no knobs	almost smooth	strongly cancellate, nodulose,	prominent subsutural and anterior spiral cord, faint spiral knobs	extended strong spiral cords, marked spiral knobs
Coloration	grayish	tan	orange-yellow	whitish	grayish	deep yellow
Distribution	southern Mozambique	Natal, southern Mozambique	Natal	Transkei, South Africa	Zanzibar Channel	Somalia

Figures 3–21. *Fusivoluta profundorum*. **3–5.** Holotype. MNHN 22816, Stn CP 3139, 1194 m, 49.0 mm. **6–7**. Paratype I, IM-2009-9489, Stn CP3139, 45.7 mm. **8–9**: Paratype II, IM-2009-9488, Stn CP3139, 44.6 mm. **10–11.** Paratype III, stn CC3158, 1220–1248m, 43.3 mm. **12–13.** Stn CP3139, 42.9 mm. **14–15.** Stn CP3139, 43.0 mm. **16–17.** Stn CP3139, 44,5 mm. **18–19.** Stn CP3145, 1408–1421 m, 55.5 mm. **20–21.** Stn CC3158, 1220–1248 m, 43.3 mm (live taken).



Figures 22–39. Living species of *Fusivoluta* (except for *F. decussata*, all the shells illustrated here are from the first author's collection). **22–23.** *F. barnardi*, off Tugela Bank, Natal, RSA, 320 m, 135 mm. **24–25.** *F. decussata*, off Mashbe River, Transkei, 700 m, 47 mm, Natal Museum (Photo D. Herbert). **26–27.** *F. clarkei*, off Maputo, Mozambique, 450–510 m, 122.3 mm. **28–29.** *F.* aff. *anomala*, Zanzibar Channel, 850 m, 47.5 mm. **30–31.** *F. anomala*, South of Ras Afun, Somalia, 420–450 m, 61.8 mm. **32–33.** *F. pyrrhostoma*, Agulhas Bank, RSA 400 m, 78.1mm. **34–35.** *F. sculpturata*, Capetown, no depth given, 27.5 mm. **36–37.** *F. blaizei*, off Cape St Blaize, RSA, *circa* 250 m, 48.2 mm. **38–39.** *F. wesselsi* Tegula Bank, Natal, RSA, 50 m, 24.6 mm.

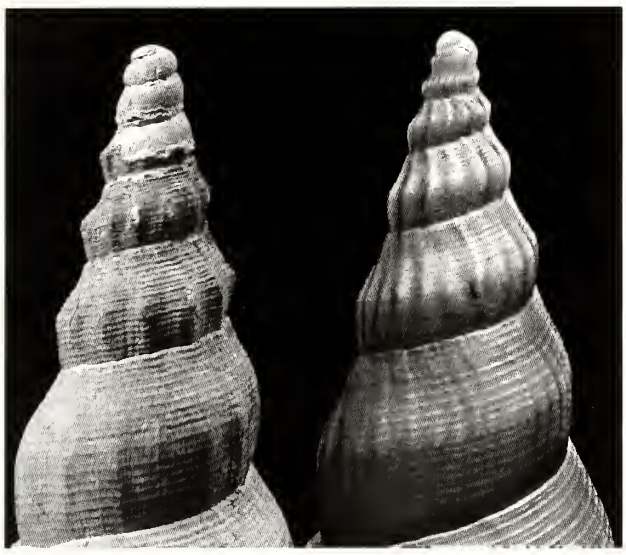


Figure 40. Comparison between the early spires of *Fusivoluta profundorum* (left) and *F. clarkei* (right).

Discussion: *Fusivoluta profundorum* shows very few variants, differing only by the strength of the axial ribs, knobbed specimens occurring mainly below 1400 m.

The genus *Fusivoluta* comprises ten East African species, of which five species, rising in successive ranges all along the east coast of Africa, must be compared with *F. profundorum*:

Fusivoluta barnardi Rehder, 1969 (Figures 22–23) from the coast off Natal, is a large shell (up to 145 mm long) with 7–8 teleoconch whorls, a high spire, axial ribs forming small nodules on the three early whorls, crossed by fine spiral lirae, becoming obsolete on the subsequent whorls giving a smooth surface. Background colour and aperture deep beige-orange.

Fusivoluta decussata Barnard, 1959 (Figures 24–25), from Transkei, is a rare species, with only 5 specimens known. It is a medium-sized, solid species (approx. 50 mm) bearing a strong cancellate sculpture, the intersection between spiral and axial cords forming nodules. The thickness of this shell, the lack of true axial ribs and its notched suture contrast with the other members of the genus. Barnard himself placed this distinctive shell provisionally in *Fusivoluta*, pending studies of its anatomy.

Fusivoluta clarkei Rehder, 1969 (Figures 26–27) from off Mozambique, is a parapatric species occurring all along the same range as *F. profundorum*, but at lesser depth, from 450 to 900 m. It is a highly polymorphic species varying in size, shape and sculpture, according to depth. The type locality (holotype DNMN 12833) is off João Belo, Gaza district in 440 m. This typical form (Figures 41–43) the closest to *F. profundorum*, thrives between 450–650 m. It differs from the latter by a large size, 75–125 mm long, an elongate-fusiform shape with high spire and relatively long anterior canal. The 2–3 first post-nuclear whorls are made angulate by nodulose axial ribs, reduced to weak axial plicae on the rest of the spire, absent on the last whorl. Numerous strong spiral cords extending onto the whole teleoconch. Columella straight or weakly concave. Background color yellowish pink, the subsutural zone slightly darker.

Between 600 to 900 m, *F. clarkei* tends to be broader, with more pronounced spiral cords (Figures 44–45). Some shells are very squat, with reduced axial ribs, and very prominent spiral sculpture, which imparts the shell a rough

Figures 41–47. Variations of *Fusivoluta clarkei*. **41.** North Natal, RSA, 350–400 m, P. Bail collection (ex Meyer collection) 70.0 mm. **42.** Mozambique, 1M-2009-9495, Stn CC3154, 19°36′ S, 36°47′ E, 636 m, MNHN, 58. 2mm. **43.** Mozambique, 1M-2009-7340, Stn CP3141, 23°33′ S, 35°55′ E, 684–698 m, MNHN, 72.8 mm. **44.** Mozambique, 750–800 m, P. Bail collection, 84.6 mm. **45.** Mozambique, Stn CP3140, 23°33 S, 36°07S, 890–900m, MNHN, 77.1 mm. **46.** Mozambique, Stn CP3148, 21°32′ S, 35°47′ E, 768–787 m, MNHN, 75.3 mm. **47.** South Mozambique, 750–800 m, P. Bail collection (ex Meyer collection), 86.8 mm.

Figure 48. Map of the estimated range of *Fusivoluta profundorum*.

cancellate surface, very similar to that of *F. decussata* (Figures 46–47). No live-taken specimens of this form have been found until now. From 900 m to 1200 m, no *Fusivoluta* have been brought up by the few dredgings operated by Mainbaza expedition, suggesting a possible depth gap between the habitat of *F. clarkei* and *F. profundorum*, subject to confirmation by future expeditions.

Fusivoluta aff. *anomala* (Figures 28–29), from off Zanzibar, is a rare species discovered during the 1980s by Russian boats operating along the Zanzibar Channel in deep water (600–800 m). Sharing the same medium size (*circa* 45 mm) and light stucture with *F. profundorum*, it differs by a turreted protoconch of 3 whorls and a very tapered spire. Sculpture of strong axial ribs, adapically attenuated, numbering 14–15 on the penultimate whorl, crossed by spiral cords divided into two parts: one subsutural, the other on the anterior third part of the body whorl, delimiting a smooth central part. Its relationship to the species below is problematic.

Fusivoluta anomala (Martens, 1902) (Figures 30–31) from off Somalia, is also a very rare species, known only from the holotype. It differs from *F. profundorum* by its solid, heavy structure, a very elongate-fusiform shape with a high narrow spire, made angulate by axial nodules (13 on the penultimate whorl), crossed by raised spiral cords. Both spiral and axial sculptures extend onto the whole teleoconch. Aperture large with the outer lip very flared. Base color yellowish-beige.

Four species are too different to warrant extensive comparison: *Fusivoluta pyrrhostoma* (Watson, 1882) (Figures 32–33) from Western Cape differs by a rough surface and its tilted raised protoconch; *Fusivoluta sculpturata* (Tomlin, 1945) (Figures 34–35) from Western Cape is a small species, under 30 mm long, with heavily sculptured surface; *Fusivoluta blaizei* (Barnard, 1959) (Figures 36–37) from Western Cape is a rather small, elongate, bicoloured shell with very high spire; *Fusivoluta wesselsi* Kilburn, 1980 (Figures 38–39) from Natal is a narrow, fusiform, small-sized specie, under 25 mm when adult.

ACKNOWLEDGMENTS

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LITERATURE CITED

Barnard, K.H. 1959. Contribution to the Knowledge of South African Marine Mollusca. *Fulgoraria blaizei*. Annals of the South African Museum 45: 28–31, text-fig. 8.

Fraussen K. and J. Rosado. 2011. The *Cantharus* group (Gastropoda: Buccinidae) on Almirante Leite Bank (Mozambique) with description of two new species and one new genus. Novapex 12: 73–79.

Huelsenbeck, J.P., F. Ronquist, and B. Hall. 2001. MrBayes: bayesian inference of phylogeny. Bioinformatics 17: 754–755.

Jovelin, R. and J.L. Justine. 2001. Phylogenetic relationships within the Polyopisthocotylean monogeneans (Plathyhelminthes) inferred from partial 28S rDNA sequences. International Journal for Parasitology 31: 393–401.

Puillandre N., Yu. Kantor, A. Sysoev, A. Couloux, C. Meyer, T. Rawlings, J.A. Todd, and P. Bouchet. 2011. The dragon tamed? A molecular phylogeny of the Conoidea (Mollusca, Gastropoda). Journal of Molluscan Studies 77: 259–272.

Rehder A.H. 1969. Two Genera of Deep Water Volutidae from South Africa. The Veliger 11: 200–209, pls 40–43, figs 1–43.

Tomlin J.R. 1945. Two South African specieds renamed. Journal of Conchology 22: 135.

A new species of *Mysella* from Patagonia (Bivalvia: Galeommatoidea)

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ABSTRACT

The poorly known diversity of the genus *Mysella* in the southwestern Atlantic is improved with the description of a new species from San Julián Bay, Santa Cruz Province, Argentina. *Mysella patagona* new species is characterized by the relative large, strikingly subquadrate, slightly inequilateral and flat shell; a cleft hinge plate, with two widely diverging teeth in the right valve, and a cylindrical internal ligament located in a deep ligamental pit. From the anatomical point of view, *M. patagona* new species is characterized by the presence of inner and outer demibranchs, with very few interlamellar junctions. The marked subquadrate shell outline easily distinguishes *M. patagona* from any other *Mysella* species currently known from the Magellan Region.

Additional keywords: Southwestern Atlantic, Southern Hemisphere, bivalves

INTRODUCTION

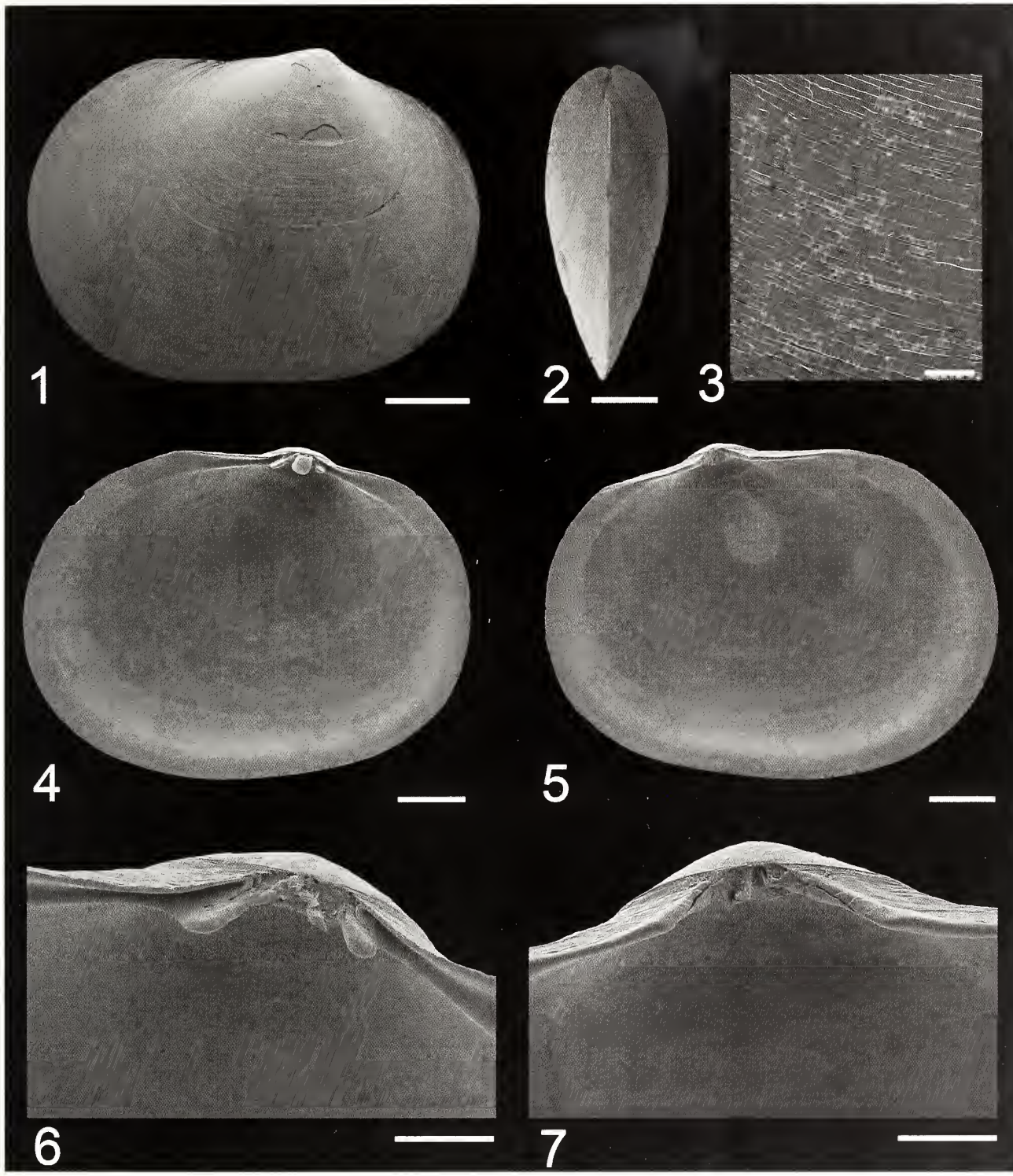
Recent contributions have described and re-described several small-sized Magellanic bivalves, helping improve the scanty attention given to this fauna in the past (Zelaya and Ituarte, 2002, 2004, 2009, 2012). Members of the genus *Mysella* are not an exception. At present, four species of *Mysella* are known from Magellanic waters: *Mysella mabillei* (Dall, 1908), *Mysella rochebrunei* (Dall, 1908) and *Mysella sculpta* Soot-Ryen, 1957, all from the Magellan Strait, and *Mysella arthuri* (Cooper and Preston, 1910) from Malvinas (Falkland) Islands.

In the past few years, mysellids from other parts of the world have been covered in several contributions (Boyko and Mikkelsen, 2002; Coan and Valentich-Scott, 2012; Passos and Domaneschi, 2006; Passos et al., 2005). Gofas and Salas (2008), after studying the type species of *Mysella* Angas, 1877, *Rochefortia* Vélain, 1878, *Rochefortula* Finlay, 1927, and *Altenaeum* Spaink, 1972, considered *Mysella* and *Rochefortia* as synonyms, instead of two separate genera as done by other authors (Coan et al., 2000). Furthermore, Gofas and Salas (2008) concluded that *"Mysella" bidentata* (Montagu, 1803), as well as other European species previously placed in *Mysella*, are not congeneric with *Mysella anomala* Angas, 1877, the type species of the genus, and introduced the genus *Kurtiella* to include them. Coan and Valentich-Scott (2012) also considered the Pacific "mysellids" from tropical West America under *Kurtiella*.

In the present paper, a new species of *Mysella* from southern Patagonia is described and fully illustrated.

MATERIALS AND METHODS

Specimens collected during low tides by sieving (1 mm mesh) portions of substratum from a tidal flat at San Julián Bay were immediately fixed in 70% ethanol. Specimens for histology were decalcified by immersion in Bouin's fixative for 8 h, rinsed in tap water, dehydrated in an ethanol series, and embedded in epoxy resin (Historesin Leica®). Sections (3.5 µm thick) were stained with hematoxylin–eosin. Voucher specimens are deposited at Museo Argentino de Ciencias Naturales (MACN) and Museo de La Plata (MLP). Linear measurements (shell length [L], shell height [H], and shell width [W]) were taken with a Zeiss Stemi 2000-C stereomicroscope with ocular micrometer.



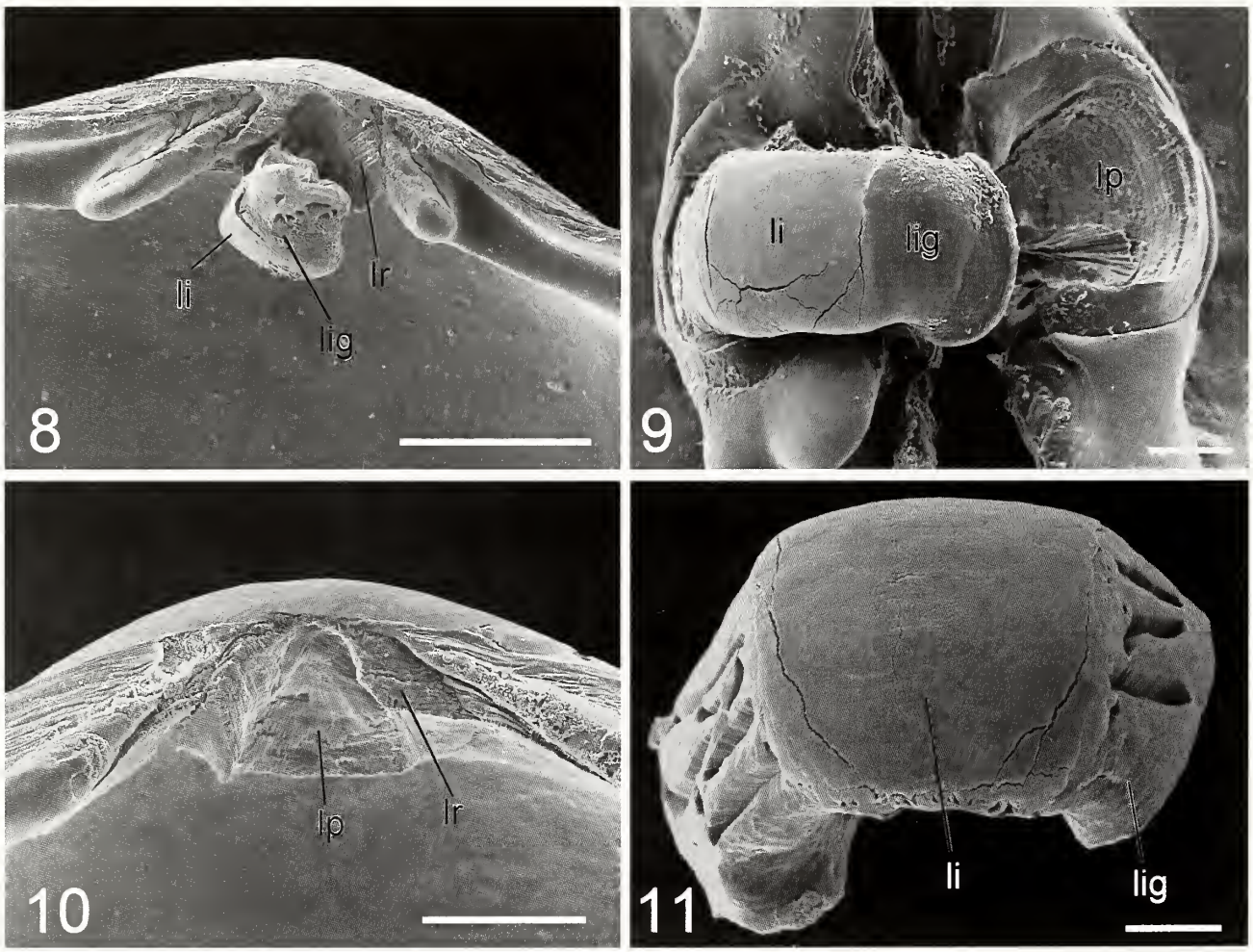
Figures 1–7. *Mysella patagona* new species: Shell morphology. **1.** Holotype, MACN-In 38865, lateral view of left valve. **2–7.** Paratypes MACN-In 38866. **2.** Posterior view. **3.** Shell surface with periostracum folds. **4.** Inner view of right valve. **5.** Inner view of left valve. **6.** Right valve, detail of hinge. **7.** Left valve, detail of hinge. Scale bars: Figure 1 = 1 mm; Figures 2, 4, 5 = 0.5 mm; Figure 3 = 20 μm; Figures 6, 7 = 300 μm.

SYSTEMATICS

Mysella patagona new species
(Figures 1–19)

Description: Shell thin, relatively large for genus (maximum observed L = 7 mm), compressed (W/H ratio = 0.50 ± 0.05, n = 15), nearly equilateral, anterior half longer (Figures 1, 2). Valves subequal. Shell outline subquadrate (H/L ratio = 0.70 ± 0.02, n = 15); beaks small, low, subcentral, opisthogyrate, slightly projecting above dorsal margin (figures 1, 4, 5). Dorsal margin about 55% of shell length, slightly flaring anteriorly, with anterior and posterior portions similar in length; anterior half straight or slightly concave, posterior half slightly curved or straight. Anterior and posterior margins wide and evenly curved, anterior higher, forming weak angles at junction with dorsal margin (figures 1, 4, 5). Ventral margin nearly straight (Figure 1), slightly curved at anterior end. Shell surface whitish, sometimes brownish in larger specimens, sculptured with very low, irregularly spaced periostracal folds, and slightly marked growth lines (Figure 3). Prodissoconch oval, length about 650 µm (n = 3), smooth.

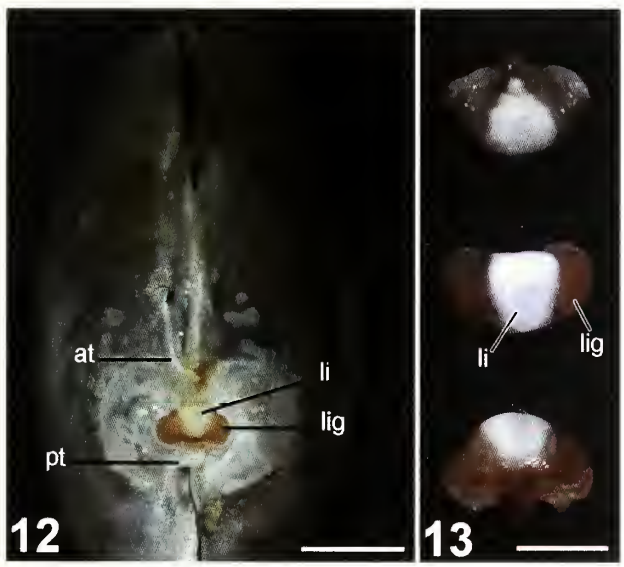
Hinge plate not solid, cleft just beneath beaks, leaving a passage for internal ligament (resilium) (Figures 6, 7, 8, 10). Right valve with two small, subequal, peg–like teeth, anterior longer and slender, posterior somewhat columnar, located on either side of resilium (Figures 4, 6, 8). Anteriorly to anterior tooth and posteriorly to posterior tooth, hinge plate margin forms low ridge delimiting with dorsal shell margin two grooves (Figures 4, 6) that accommodate margin of opposite valve (Figures 5, 7). Left valve edentulous, with dorsal margin moderately thickened on each side of resilium, forming short lamellae that interlock with grooves in right valve (Figures 5, 7). Ligamental pit



Figures 8–11. *Mysella patagona* new species: Ligament and ligamental pit. **8.** Detail of right valve hinge showing teeth, ligament and deep ligamental pit. **9.** Ventral view of ligament and ligamental pit. **10.** Detail of ligamental pit in left valve. **11.** Detail of ligament with lithodesma. Abbreviations: **li,** lithodesma; **lig,** ligament; **lp,** ligamental pit; **lr,** ridge of ligamental pit. Scale bars: Figure 8 = 200 µm; Figures 9, 10 = 100 µm; Figure 11 = 50 µm.

(resilifer) deep. In both valves, two strong, vertical pre- and post-ligamental ridges delimiting ligamental pit, are connected laterally with hinge plate (Figures 8, 10). Ligament strong, cylindrical (Figure 9), with a wide, somewhat trapezoidal, calcified area, forming very thin ventral shield, lithodesma (Figures 11, 12, 19), that extends to cover partially anterior and posterior portions of ligament (Figures 13, 19).

Anatomy: Mantle border thin, nearly smooth; widely open in a long inhalant–pedal aperture extending for about 3/4 of mantle margin length, separated from small posterior exhalant aperture by short presiphonal suture. Short, slightly pointed papillae present and restricted to anterior part of inhalant–pedal aperture and posterior to presiphonal suture (Figures 14, 15). Ctenidia non-plicate, inner and outer demibranchs present, outer one reflected upward (Figure 14), with few interlamellar junctions, mainly restricted to lower portion of ctenidia (Figure 16). Ctenidial axis almost parallel to dorsoventral axis. Outer demibranch small, less than half length of inner demibranch, with up to 40 filaments approximately parallel to antero-posterior axis (Figure 14). Ascending and descending lamellae of outer demibranch equally developed. Inner demibranch with 50 obliquely directed filaments (in larger studied specimen); ascending lamella approximately half length of descending lamella. Tips of filaments of ascending lamellae attached to visceral mass tegument by tissue junctions (Figure 16). Left and right inner demibranchs fused at posterior end at level of presiphonal suture (Figure 15). Brooding in gills was observed in one specimen (ca. 7 mm length) collected in April (Austral Autumn). Labial palps with 10 sorting ridges. Ventral surface of presiphonal suture ciliated, forming a groove when valves are closed (Figures 15, 18). Foot large, compressed laterally, with well developed posterior heel (Figure 14). Anterior part of foot heavily ciliated. Transverse section of anterior and posterior adductor muscles ovate, subequal, anterior adductor with posterior indentation (Figure 14). Anterior pedal retractor strong. Prominent byssal gland opening in a ciliated byssal groove (Figure 17).



Figures 12–13. *Mysella patagona* new species: Ligament and lithodesma. **12.** Hinge and ligament from ventral view. 13. Ligament and lithodesma: anteroventral view (upper), ventral view (centre), posteroventral view (bottom). Abbreviations: **at,** anterior right tooth; **li,** lithodesma; **lig,** ligament; **pt,** posterior right tooth. Scale bars: Figure 13 = 0.5 mm; Figure 14 = 0.2 mm.

Habitat: *Mysella patagona* new species lives in lower intertidal and shallow subtidal mud-sandy beaches: 46–68% mud (silt + clay), 31–53% fine sand, and 2.5–4.0% organic matter content. *Mysella patagona* is a conspicuous species of the infaunal assemblage dominated by the bivalve *Darina solenoides* (King, 1832), the amphipod *Ampelisca* sp., and the polychaetes *Scolecolepides uncinatus* Blake, 1983 and *Eteone sculpta* Ehlers, 1897. *Mysella patagona* showed abundances of up to 30,000 ind.m^{-2}, representing in some areas the dominant species of the infaunal assemblage (J.P. Martin, unpublished data).

Type Locality: 49°17′30″ S, 67°43′22″ W, northwest of San Julián Bay, Santa Cruz Province, Argentina.

Material Examined: Holotype (MACN–In 38865) and 15 paratypes from the type locality (4 MACN–In 38866, mounted for SEM; 5 MACN–In 38866, ethanol preserved specimens; 5 MLP 13635, dry specimens).

Etymology: The species name, a noun in apposition, honors to Patagones, the name given by Spaniard explorers to the ancient people who inhabited vast regions of the Argentine southern littoral.

Distribution: Only known from the type locality.

Remarks: *Mysella patagona* new species is similar to *Mysella rochebrunei* (Dall, 1908), differing by its larger size and by having a markedly subquadrangular shell outline with straight, nearly horizontal (not sloping) anterior and posterior parts of dorsal margin, ventral margin nearly straight, slightly curve at anterior end, and more prominent beaks. The larger size and subquadrate shell outline easily separate *Mysella patagona* new species from the other mysellid species reported from the Magellan Region: *Mysella mabillei* (Dall, 1908) from eastern Magellan Strait, *Mysella arthuri* (Cooper and Preston, 1910) from the Malvinas (Falkland) Islands, and *Mysella sculpta* Soot-Ryen, 1957, from the Magellan Strait, as well as from the Antarctic species *Mysella charcoti* (Lamy, 1906) and *Mysella narchii* Passos and Domaneschi, 2006; all of these have a strikingly trigonal-ovate and markedly inequilateral shells. Furthermore, *Mysella arthuri* has only one, the anterior, cardinal tooth in the right valve.

Kurtiella Gofas and Salas, 2008, was based on "the complete regression of the hinge plate beneath the umbones",

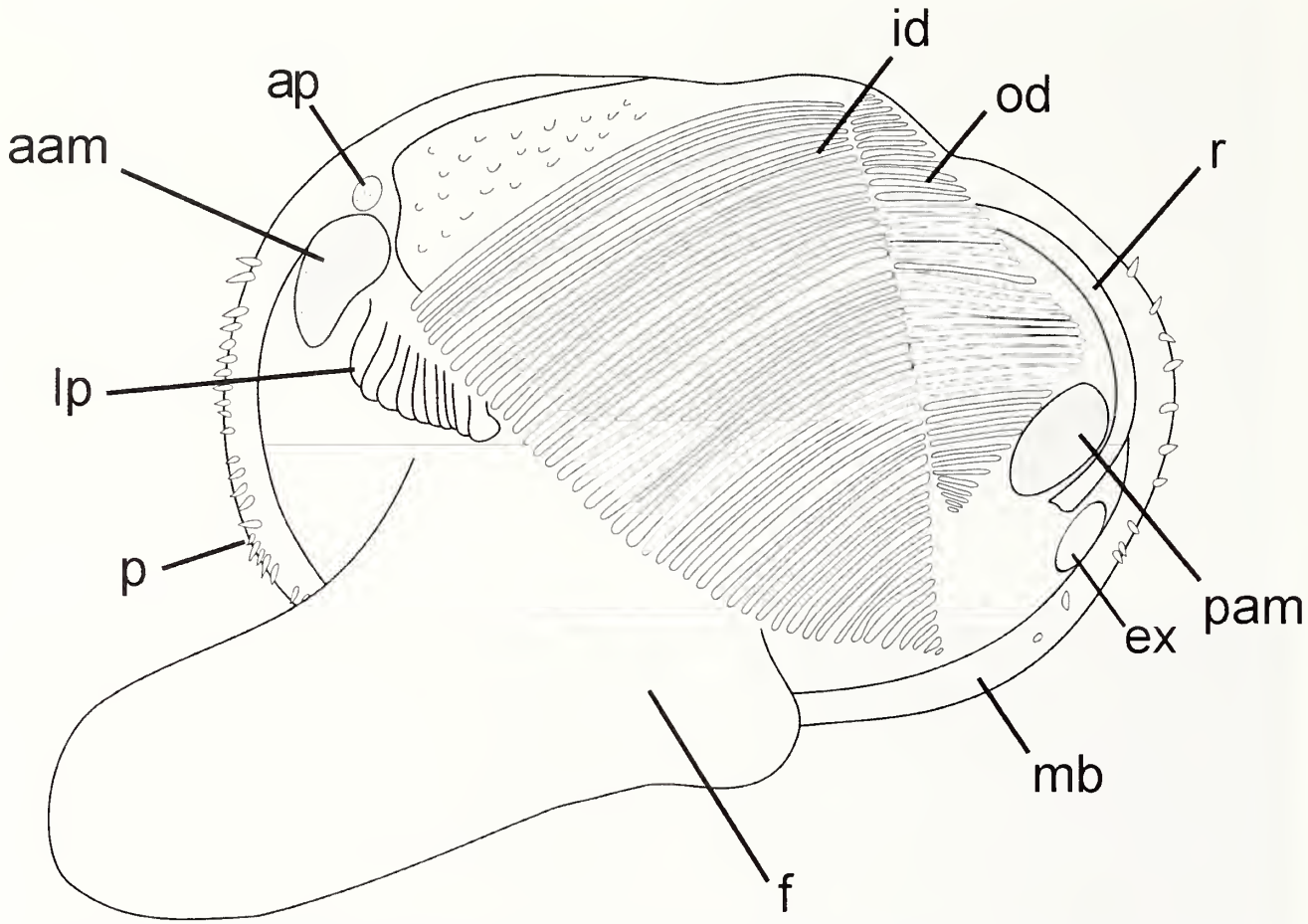
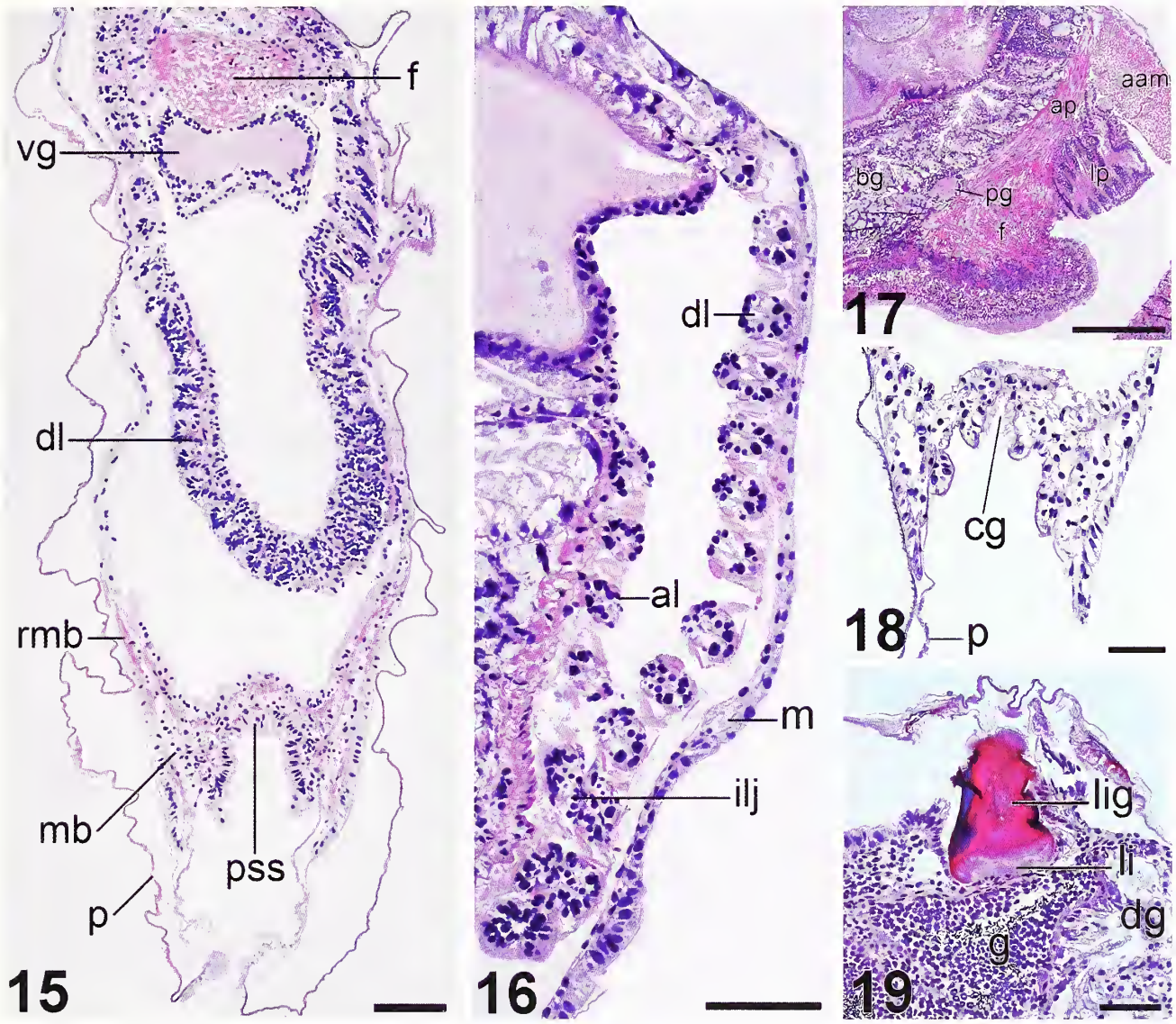


Figure 14. *Mysella patagona* new species: Gross anatomy, left lateral view, left shell and mantle removed. Abbreviations: **aam,** anterior adductor muscle; **ap,** anterior pedal retractor; **ex,** exhalant aperture; **f,** foot; **id,** inner demibanch; **lp,** labial palp; **mb,** mantle border; **od,** outer demibranch; **p,** papillae; **pam,** posterior adductor muscle; **r,** rectum.

a condition not present in *Mysella anomala*, the type of the genus in which the solid hinge plate underlies a not outstanding ligamental pit. In *Kurtiella* species the internal ligament is connected to the shell. The latter condition is more similar to that found in *Mysella patagona*, in which, however, the space below the beaks is occupied by a strong resilifer which is flanked by two strong lateral ridges. This condition is not seen in the type of *Mysella* nor in *Kurtiella* (see for example the hinge of *K. bidentata* (Montagu, 1803) illustrated by Gofas and Salas (2008: fig. 7 E, F). Anterior and posterior teeth of right valve are subequal in *M. patagona* as in *Kurtiella* species, but while in *Kurtiella* only the inner demibranchs are present, *M. patagona* new species has both inner and outer demibranchs. For the above reasons, the generic location of the new species is difficult, and we prefer to be conservative, placing *Mysella patagona* provisionally under *Mysella*.

The presence of a lithodesma associated with the internal ligament, a structure well known for many, but not all anomalodesmatans (Harper et al., 2006), and reported by Morton (1980) in some montacutids as *Mysella (Montacutona) compacta* (Gould, 1861) and *Mysella (Montacutona) olivacea* (Habe, 1959), was also reported by Gofas and Salas (2008) as one of the diagnostic characters of *Kurtiella* (originally placed in Montacutidae).

As recently discussed by Boyko and Mikkelsen (2008), the family-level relationships in the Galeommatoidea are not clear, nor they have been revised for relationships at the family and genus levels. Montacutidae is the family to which *Mysella* was traditionally assigned. *Mysella patagona* new species agrees in general terms with montacutid anatomy, differing in having both inner and outer demibranchs, an important character at the family level. Coan et al. (2000) and Coan and Valentich-Scott (2012), not finding consistent characters to separate the Erycinidae, Kellidae and Montacutidae, considered them under a single family, Lasaeidae, a criterion also followed by Bieler et al. (2010).



Figures 15–19. *Mysella patagona* new species. Histology. **15.** Transverse section showing posterior fusion of descending lamellae of inner demibranch and presiphonal suture. **16.** Detail of inner demibranch. **17.** Sagittal section of foot. **18.** Detail of posterior mantle fusion. **19.** Sagittal section with detail of ligament. Abbreviations: **aam,** anterior adductor muscle; **al,** ascending lamella of inner demibranch; **ap,** anterior pedal retractor; **bg,** byssus gland; **cg,** ciliated groove; **dg,** digestive gland; **dl,** descending lamella of inner demibranch; **f,** foot; **g,** gonad; **ilj,** interlamellar junction; **li,** organic matrix of lithodesma; **lig,** fibrous portion of ligament; **lp,** labial palp; **m,** mantle; **mb,** mantle border; **p,** periostracum; **pg,** pedal ganglion; **pss,** presiphonal suture; **rmb,** retractor muscle of mantle border; **vg,** visceral ganglia. Scale bars: Figure 15 = 200 µm; Figures 16, 18 = 50 µm; Figures 17, 19 = 100µm.

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LITERATURE CITED

Boyko, C.B. and P.M. Mikkelsen. 2002. Anatomy and biology of *Mysella pedroana* (Mollusca: Bivalvia: Galeommatoidea) and it commensal relationship with *Blepharipoda occidentalis* (Crustracea: Anomura: Albuneidae). Zoologischer Anzeiger 241: 149–160.

Bieler, R., J.G. Carter and E.V. Coan. 2010. *Classification of Bivalve families*. Pp. 113-133, in: Bouchet, P. and J.P. Rocroi, (2010). Nomenclator of Bivalve Families. Malacologia 52: 1–184.

Coan, E.V., P.V. Scott and F.R. Bernard. 2000. Bivalve seashells of western North America: marine bivalve mollusks from Arctic Alaska to Baja California. Santa Barbara Museum of Natural History Monographs 2: 1–764.

Coan E.V. and P.V. Valentich Scott. 2012. Bivalve seashells of tropical West America: marine bivalve mollusks from

Baja California to Northern Peru. Santa Barbara Museum of Natural History Monographs, 6, 1258 pp.

Passos, F.D. and O. Domaneschi. 2006. A new species of *Mysella* Angas, 1877 (Bivalvia: Galeommatoidea) from Admiralty Bay, King George Island, South Shetlands, Antarctica, with data on its biology and functional anatomy. Polar Biology 29: 389–398.

Passos F.D., O. Domaneschi and A.F. Sartori. 2005. Biology and functional morphology of the pallial organs of the Antarctic bivalve *Mysella charcoti* (Lamy, 1906) (Galeommatoidea: Lasaeidae). Polar Biology 28: 372–380.

Gofas, S. and C. Salas. 2008. A review of European "*Mysella*" species (Bivalvia, Montacutidae), with description of *Kurtiella* new genus. Journal of Molluscan Studies 74: 119–135.

Harper, E.M., H. Dreyer, and G. Steiner. 2006. Reconstructing the Anomalodesmata (Mollusca: Bivalvia): morphology and molecules. Zoological Journal of the Linnean Society 148: 395–420.

Morton B. 1980. Some aspects of the biology and functional morphology (including the presence of a ligamental lithodesma) of *Montacutona compacta* and *M. olivacea* (Bivalvia: Leptonacea) associated with coelenterates in Hong Kong. Journal of Zoology 192: 431–455.

Zelaya, D.G. and C. Ituarte. 2002. The identity of *Waldo parasiticus* (Dall, 1876) and description of *Waldo trapezialis* new species (Bivalvia, Galeommatoidea). The Nautilus 116: 109–117.

Zelaya, D.G. and C. Ituarte. 2004. The genus *Neolepton* Monterosato, 1875 in southern South América (Bivalvia: Neoleptonidae). Journal of Molluscan Studies 70: 123–137.

Zelaya, D.G. and C. Ituarte. 2009. A new species of *Pseudokellya* Pelseneer, 1903 from the Southern Ocean (Bivalvia: Cyamiidae). The Nautilus 123: 1–8.

Zelaya, D.G. and C. Ituarte. 2012. *Tellimya* new species: First record of *Tellimya* Brown, 1827 in South America (Bivalvia: Montacutidae). Malacologia 55: 173–182.

The dating of modern books and their included taxa

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ABSTRACT

Disparities in dating the molluscan taxa introduced in three books by E. J. Petuch are discussed and reconciled. Also addressed is the potential problem in using the copyright date or the Library of Congress Control Number for dating nomenclatural acts that are published in books.

INTRODUCTION

The publication dates of three books written by E. J. Petuch, either as sole or senior author, have been variously treated in the literature. As more than one hundred new molluscan taxa are introduced in the three works, these have been investigated in an attempt to determine their correct date of publication. These books are listed and treated individually herein.

Information developed about the dating of modern books is included as it affects numerous works. It may surprise some people that the copyright year date in a book is not necessarily the year of publication. An attempt is made herein to describe the various ways through which publication dates are determined, correctly and incorrectly. Unfortunately, there is not a simple way to precisely determine publication dates.

A fourth book by the same author, containing no new nomina, is also treated as it has a misleading copyright date.

Abbreviations used in the text are: CIP – Cataloging-in-Publication Data; ICZN – International Code of Zoological Nomenclature; ISBN – International Standard Book Number; LCC – Library of Congress Classification; LCCN – Library of Congress Control Number; LOC – Library of Congress; MARC – Machine-Readable Cataloging record.

BOOK PRINTING AND PUBLICATION DATA

Information on the production and publication dates of books usually appears on what was once called a colophon page located at the end of the book. Items normally listed are the International Standard Book Number (ISBN), Library of Congress Control Number (LCCN), Library of Congress Classification (LCC), and other items comprising Cataloging-in-Publication Data (CIP). In modern works such data is on the verso of the title page. In some books this information appears in several areas of the page, usually headed by the copyright date which is not part of the CIP. In most books, especially those published by large publishing firms, the CIP appears in a block headed "Library of Congress Cataloging in Publication Data" while in others it appears without a heading. This LOC data is utilized by most librarians as the basis for their library records and catalogs.

It is difficult to believe that cataloguing a book could be so involved or esoteric until one makes an effort to understand the terms and numbers involved. Only the barest essentials will be mentioned here. In-depth knowledge of the system and its ramifications would require years of study.

Usually the first number to appear in the LOC block is the ISBN. The ISBN consists of 10 or 13 digits, with some books having both. These numbers are sold to publishers who then assign them to their books. This is a monopoly, with single numbers now costing $125. However, blocks of 10 can be purchased for $250 and 100 numbers cost only $575. The ISBN is intended for the benefit of booksellers, not to establish the date of publication. In order for a number to be properly placed into use after it has been assigned to a book, the publisher must report such use to R. R. Bowker, the database of record for the ISBN Agency. Bowker's *Books in Print* can be searched only by subscription and should not be confused with an online ISBN search which can be made at http://www.isbnsearch.org. Such search will yield a description of the book and links to booksellers who have it available.

The LCC (what many would refer to as the "Call Number") starts with a letter or letters (for science books it is Q) and does not involve date. Following the LCC, usually separated by a wide space or on a separate line, is the LCCN. This is a number of seven to ten digits, the first two or four indicating the year cataloging began and a number assigned, which may, or may not, coincide with the year of publication. This data is taken neither from the book nor from the ISBN form, but from a separate CIP form submitted by the publisher. Not all books

having a ISBN also have a LCC or a LCCN (e.g., Petuch and Sargent 2012).

A search for a book in the LOC on-line catalog returns a detailed listing similar to most library listings. At the top there are several additional options including "Full Record" and "MARC Tags." Clicking on the latter brings up a detailed history of the cataloging of the item but the tag numbers are not explained. However, they are explained in large part on the internet. These tags are sometimes important as one tag indicates the last date a catalog entry was accessed and checked or emended (although the changes are not noted) and which is usually the date that an actual book was inspected and not just a form. However, due to back logs a book might wait a considerable time before being checked, if at all. More about MARC can be found at http://www.loc.gov/marc/umb/um01to06.html.

The LOC data block also contains a date, usually preceded by a "c" in the form c1988. The "c" is used in lieu of the copyright symbol [©] and is taken from the CIP form. It might as well be considered an abbreviation for the Latin *circa* which would be appropriate, especially considering that it is sometimes used for books that are not registered at the Copyright Office (e.g. Petuch 2007). The LOC cannot place an absolute publication date in their data unless the book is actually imprinted "Published (date)." As a LOC specialist wrote me, "Publishers do not care about a publication date per se."

Not included in the LOC block of data is the copyright date, usually in the form of: © 2010 Publishers Name. This date is unfortunately meaningless for determining the date of publication. In practice a book with a © 2010 date could have been published in 2009 or 2010, or possibly even in some other year. There will be more about this under the discussion of the dating of *Cenozoic Seas*.

Usually on the colophon page, but not in the LOC data block, are one or two strings of numbers, placed there by the printer, which are referred to as the Printer's Key. An example is: 93 92 91 90 89 88 5 4 3 2 1. The lowest number in the double digit series is the year of printing and the lowest number of the single digits is the printing number. In this example it is a 1988 1st printing. There is no "rule" as to how many digits are used in each series, or whether they should be in ascending or descending order. These data, inserted by the printer, have no real bearing on publication date.

In the following section book titles are in bold type and the block of text immediately below the book title is the LOC Catalog Data.

BOOKS DATED

Field guide to the ecphoras. [E. J. Petuch]

LOC catalog data (in part): LCCN 88035283; Personal name: Petuch, Edward J.; Published/Created: Charlottesville, Va., U.S.A.: Coastal Education & Research Foundation, c1988; Description: 140 p.: ill.: 22 cm.; ISBN 0938415034; LCC QE809.M85 P48 1988.

Not included in the pagination are the title and contents pages [iv] and the front and rear covers which bear figures with captions within [iv].

In addition to the LOC data this book bears the imprint "Copyright© 1988 by the Coastal Education & Research Foundation." However, the book is not registered with the U.S. Copyright Office as shown by a search at http://www.copyright.gov/records/.

The Printer's Key in this book is 94 93 92 91 89 88 5 4 3 2 1. The lowest of the first six numbers indicates the year of printing as 1988. This indication is invalid for dating as the printing process may not have actually been completed in 1988 as scheduled. The other series of numbers shows that this is the 1st edition.

The MARC tags for this book show that the record was started on 19 December 1988 (MARC tag line 008) from CIP data (tag line 906). MARC tag line 005 shows that the last transaction was on 20 June 1989, considered to be the date that a book was checked against the record.

At the bottom of the verso of the Contents page is the printed statement "Species validation date: 15 February 1989." There is no provision in any edition of the International Code of Zoological Nomenclature (ICZN) for a "validation date" to be determined in such fashion as all of the new taxa in any work must date from the actual publication date. This is a matter of concern as three genera and 22 species names appear as new in the *Field Guide*.

The ISBN is of no value in establishing a date as will be explained in a Discussion at the end of this paper. In a futile search for definitive dating it has been noted that at least two book dealers list the publication date as January 1, 1989 with one even adding "Sun." to that date. The origin of this date has not been established.

The third line of the *Books in Print* entry for *Field guide to the ecphoras* is "Publication Date: United States: 01 Oct 1989". This cannot be correct as a copy at hand was received on 27 March 1989. Further down in the listing is a line for "Date last updated", stated to be "16 Aug 2008". A search of Amazon.com by ISBN returns an entry for the book listing it as "(Jan 1989)" but it is not in stock. The source of this date cannot be determined. A search for this book at www.isbnsearch.org by ISBN returns "Warning: Invalid argument supplied ..." with what appears to be a link but is nonfunctional even when copied and pasted.

The publication date in most library catalogues mimics the LOC listing, with date as c1988. It is dated 1988 by Donovan (1991: 52), Ward (1992: 143; 2008: 393), and on the U. S. Geological Survey National Geologic Map Database (http://ngmdb.usgs.gov/Prodesc/proddesc_91675.htm). It was also dated as 1988 by Petuch (1988: 80) in Literature Cited. However, the date 1989 has been consistently used by Petuch in his later works.

This is the last of four books, all by Petuch, published by Coastal Education & Research Foundation, Inc. (CERF). Advertisements for their books were placed in 1988 and 1989 issues of the quarterly *American Conchologist*.

As late as the June 1989 issue the *Field Guide* was not among those listed. It was first advertised in the September 1989 issue where it was included with the other three. Dr. Charles W. Finkl, President of CERF, advises that records that would show publication dates no longer exist. The *Journal of Coastal Research*, published by CERF, did not list it as a publication until Volume 5 Number 2 [Spring 1989] where it is listed as "(1989)".

As no record of this work being available in 1988 has been located, and the only printed date appearing therein aside from the copyright date is the "validation date" of 15 February 1989, that date must be accepted as the publication date of this book. The copy at hand was received on 27 March 1989 but it is not known if it was ordered prepublication or after it was known to be available. No prepublication advertisements have been located.

It should be noted that "ecphoras" in the title is neither italicized nor capitalized, being used as a vernacular as explained by Petuch in his Introduction.

Cenozoic Seas. The view from eastern North America. [E. J. Petuch]

LOC catalog data (in part): LCCN 2003065367; Personal name: Petuch, Edward J.; Published/Created: Boca Raton, Fla.: CRC Press, c2004; Description 308 p.: ill.: 26 cm.; ISBN 0849316324; LCC QE39.5.P25 P45 2004,

The above LOC data is taken from the LOC website. The LCC printed in the LOC data block in the book differs by ending in 2003.

Not included are introductory pages [xii].

Although the book bears an imprinted copyright date of 2004, the publisher's web site showed it as having been published on 29 December 2003. Contact with the publisher brought a communication, dated 21 January 2004, from John Sulzycki, Senior Editor of CRC Press, advising that "12/29/03 was the actual date of publication."

An explanation of the difference in dates was offered to Dr. M. G. Harasewych by Mr. Sulzycki in June 2012 when he confirmed the 2003 publication date. He wrote that: "This copyright issue has come to be because of the modern day book publishing convention of giving books the following year copyright date if they publish July 1 or after. In the case of *Cenozoic Seas*, it was an unfortunate oversight that the copyright date was not the year of publication. We do that for books where we are aware that they include new species and higher taxa. It is our fault as a publisher and we bear final responsibility for this mistake with *Cenozoic Seas*. The copyright date should have been 2003 since the book published in December, 2003." The Copyright Date is listed as 29 December 2003 by the U.S. Copyright Office.

Notice of the 2003 publication date was sent by email to Dr. Petuch by this author on the same day that it was received, 21 January 2004, suggesting that he have a small notice printed in several journals noting that his new taxa (12 genera, 38 species) should be dated 2003 instead of 2004. Such action was never taken and the new taxa have been consistently dated as 2004 by all later workers, including Petuch.

Under ICZN Article 21.4 the new taxa in this work must date from 29 December 2003.

Molluscan paleontology of the Chesapeake Miocene. [E. J. Petuch and M. Drolshagen]

LOC catalog data (in part): LCCN 2009011500; Personal name: Petuch, Edward J.; Published/Created: Boca Raton: CRC Press, c2010; Related names: Drolshagen, Mardie, 1952-; Description: xvii, 160 p.: ill, maps; 27 cm. + 1 CD-ROM (4 ¾ in.); ISBN 9781439811597 and 1439811598; LCC QE801.P439 2010.

The only date printed in this book is on the copyright/colophon page where the copyright date is 2010. However, the LCCN 2009011500 indicates that cataloging began in 2009. There are no other dates. The publisher's web site lists the publication date as 19 August 2009. The copy at hand was shipped from Amazon on 22 August 2009.

Other evidence for publication in 2009 exists in a newspaper article (Chowning, 2009) that describes the book, mentions people for whom species were named, and includes a photograph of the book on a bench with fossils.

This book is not registered with the U.S. Copyright Office.

Despite having been published in 2009, there is no internal evidence in the book for that date. All American libraries checked in a survey of on-line library catalogues have the publication date listed as "c2010". The only library catalogue giving a date of 2009 is that of the Natural History Museum, London.

David Williamson of the Library of Congress has kindly provided (personal communication, 3 August 2012) an explanation of the post-dated copyright date: "Regarding the c2010 thing, towards the fall publishers start putting the copyright date for the next year. It's a tax thing as I understand it.... Since there is nothing that actually says published 2009, we have to use c2010 as the inferred date of publication."

The only citation of this recently published work found is in a review by Allmon (2011) where it is dated as 2010. No record of any of the taxa in this recently published book being cited has been found.

It is indisputable that the publication date is 19 August 2009 and the two new genera and 28 new species must be dated 2009.

The Geology of the Florida Keys and Everglades. [E. J. Petuch]

Not listed by LOC or Copyright Office. Published by Thomson, Mason, Ohio. viii + 84 p.

The copyright date of this book is 2008 but the Printer's Key indicates a 2007 printing date. This is confirmed by an ISBN search that returns December 2007 as the date of publication. The book bears ISBN 9781426630613 and 1426630611.

This book is not registered with the U.S. Copyright Office.

This attractive small book has no new taxa but has excellent photographs of lower Florida habitats and environments as well as dozens of full page color plates of fossil mollusks. It is unusual to depict fossil mollusks in color but the result is startling when compared with previously published black and white figures of the same specimens. The color and shading create a pleasing effect that is almost three-dimensional.

A request to Thomson for information about the actual publication date remains unanswered. As no new taxa are involved the date is rather immaterial, but for citation purposes it is here considered that the publication date is December 2007.

DISCUSSION

No mention has been found in the malacological literature of the fact that the copyright date of a book is not always the date of publication.

It would be reasonable to assume that a publication date used by a bookseller in combination with an ISBN is the date reported by the publisher. It must be further assumed that the publisher reported the true date of publication. However, it should be remembered that notification to Bowkers of assignment of a number to a book, submission of a CIP form to the LOC, and the submission of a form to the Copyright Office, all often occur prior to actual publication. It is the publisher's data, as reported on a CIP form, which is normally used by the LOC to generate the LOC data used by librarians. As demonstrated by the confusing listings cited above, these assumptions should be made only when no other evidence is available.

The Copyright Dates listed by the U.S. Copyright Office would intuitively be the same as the publication dates. Unfortunately, they are no more accurate than the © or c dates imprinted within the books. In fact, the U.S. Copyright Office data may include errors of a different type. While checking the Copyright Catalog for data on the books discussed herein, another Petuch work came to attention. Published in 1997 with the title *Coastal Paleoceanography of eastern North America (Miocene – Pleistocene)*, it is registered, with a copyright date of 1996 from a document dated "27Sep95", under the title *Paleoceanography of eastern North America (Miocene to Holocene)*. It would appear that the title was changed and the publisher did not notify the Copyright Office.

The practice of describing new taxa and other nomenclatural acts in commercial books has long been frowned upon by many in the malacological community, especially when new taxa appear in an appendix to a basically non-taxonomic work. There are numerous reasons for such objection, among them being lesser (or absent) peer review in the book business for systematic portions of a book and the danger of reissuing later printings without proper understanding on the part of readers of potential nomenclatural implications.

This note is not intended to address the problems with the definition of various terms ("date of publication specified"; "existence as a published work"; etc.) within Chapter 5 of the International Code of Zoological Nomenclature. The works discussed herein must be dealt with under Article 21.4 which treats cases where "the date of publication in a work is found to be incorrect." The ambiguous portion of that Article, "in existence as a published work", is much too subjective for comment here as "published work" does not mean the same to everyone. A publisher's statement of publication date, by letter or on web site, when available, must be interpreted as being equal to that date being printed in the book.

The problem of misdating or non-dating in malacological literature is not new as many dating problems are found in the older literature. One example usually mentioned in this context is that of Anton (1838), where the title page is imprinted 1839 but a printer's date in the back is 1838. This was clarified when an 1838 review of the work was located (Cernohorsky, 1978). In the modern literature, this problem usually exists only in books published by firms that are not accustomed to publishing books that include new zoological taxa. In such cases, there is no proper understanding of the implications of nomenclatural priority and the constraints presented by an incorrect or nonexistent publication date. This problem is not restricted to small publishers but afflicts such larger firms as CRC and Princeton University Press. The latter firm published the important work "*Seashells of southern Florida ... Bivalves*" by Mikkelsen and Bieler, with "Copyright © 2008" and complete Library of Congress Cataloging-in-Publication Data. That data included a LCCN indicating a 2007 date. The actual publication date was November 2007, as was pointed out by the authors (who have a policy of not introducing new taxa in such book publications).

The book industry, including printers, publishers, distributors and sellers have no real interest in accurate publication dates. David Williamson of the LOC wrote (personal communication, 3 August 2012) that "Publishers do not care about a publication date per se. They are interested in the date it is released to the public for sale (which is not given in the book) and the date of the copyright in case of litigation. Other than that there is very little interest in a true publication date." Even publishers can't agree on what that means, I work with them on a data committee and they go around and around on what the definition is—date of printing? Date of shipping to the store? Date it goes on sale?" This question is incompletely addressed in ICZN Chapter 5.

An entirely different problem with determining date of publication is found in a work by Petuch and Sargent (2012), where the only printed date is demonstrably a year earlier than the actual date of publication, and has neither a LCCN nor ISBN. That dating problem was addressed by Petit (2012).

For works already published, we will have to continue to do the best we can to establish publication dates where none is stated. For the future, it is incumbent upon those introducing new taxa or nomenclatural acts to be sure that they are publishing in a journal or series that is known to place the publication date in the work itself. If an author's work is to be published by a firm not accustomed to handling scientific books and papers involving time-sensitive items, the author should ensure that the publication date is shown as such in the work.

CONCLUSIONS

It is here considered that the correct dates of publication for the first three works discussed are: *Field guide to the ecphoras*, 1989, and not 1988 as sometimes stated; *Cenozoic Seas*, 2003, and not 2004 as shown in the CIP and in subsequent literature; *Molluscan paleontology of the Chesapeake Miocene*, 2009, and not the copyright date of 2010. It follows, of course, that these dates must apply to the considerable number of new names introduced in them. The fourth work, *The geology of the Florida Keys and Everglades*, without new taxa, dates from 2007 and not the copyright date of 2008.

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LITERATURE CITED

Allmon, W.D. 2011. Review of: Molluscan Paleontology of the Chesapeake Miocene, by Edward J. Petuch and Mardie Drolshagen, 2010. Palaios, DOI: 10.2110/palo.2011.BR64.

Anton, H.E. 1838. Verzeichniss der Conchylien welche sich in der Sammlung von Hermann Eduard Anton befinden. Eduard Anton, Halle. xvi + 110 pp. [Imprinted 1839 but published in 1838. See Cernohorsky 1978.]

Books in Print. 2012. *Books in print*. [http://www.booksinprint2.com] As this is a subscription database, only the "root" URL is shown.

Cernohorsky, W.O. 1978. The date of publication of Anton's "Verzeichniss der Conchylien". The Veliger 20: 299.

Chowning, L.S. 2009. Local shells could be over 20 million years old. Southside Sentinel (Urbanna, VA) for November 19, 2009, p. 2.

Donovan, S.K. 1991. Review: "New Caribbean Molluscan Faunas", "Field Guide to the Ecphoras," and "Neogene History of Tropical American Mollusks," by Edward J. Petuch. Journal of the Geological Society of Jamaica 28: 52–54.

International Commission on Zoological Nomenclature 1999. International Code of Zoological Nomenclature. Fourth edition. I.T.Z.N., London. xxix + 306 pp.

Mikkelsen, P.M. and R. Bieler. 2007. Seashells of southern Florida: living marine mollusks of the Florida Keys and adjacent regions. Bivalves. viii + 503 pp. Princeton University Press, Princeton and Oxford. [Copyright date 2008; published November 2007]

Petit, R.E. 2012. A review of Rare and Unusual Shells of Southern Florida (Mainland, Florida Keys, Dry Tortugas) by Edward J. Petuch and Dennis M. Sargent. Conchologia Ingrata 8: 1–9.

Petuch, E.J. 1988. New gastropods from the Maryland Miocene. Bulletin of Paleomalacology 1: 69–80.

Petuch, E.J. 1989. Field guide to the ecphoras. The Coastal Education & Research Foundation, Inc., Charlottesville, Virginia. 140 pp. [imprinted "Species validation date: 15 February 1989"] [listed in 1988: 80 as "1988" and "144 pp."] [Review: Donovan, 1991]

Petuch, E.J. 1997. Coastal Paleoceanography of eastern North America (Miocene – Pleistocene). Kendall/Hunt Publishing Company, Dubuque, Iowa, vii + 373 pp.

Petuch, E.J. 2003. Cenozoic Seas. The view from eastern North America. CRC Press, Boca Raton, Florida. [xii] + 308 pp. (98 plates included in pagination) [Review: Allmon, 2005]

Petuch, E.J. 2007. The Geology of the Florida Keys and Everglades. Thomson, Mason, Ohio. viii + 84 p.

Petuch, E.J. and M. Drolshagen. 2009. Molluscan paleontology of the Chesapeake Miocene. CRC Press, Boca Raton, Florida. xviii + 160 p. (+ CD). [Review: Allmon, 2011]

Petuch, E.J. and D.M. Sargent. 2012. Rare and unusual shells of Southern Florida (Mainland, Florida Keys, Dry Tortugas). Conch Republic Books, Mount Dora, Florida. 189 pp. (9 February)

Ward, L.W. 1992. Molluscan biostratigraphy of the Miocene – Middle Atlantic Coastal Plain of North America. Virginia Museum of Natural History, Memoir 2, 220 pp.

Ward, L.W. 2008. Synthesis of paleontological and stratigraphic investigations at the Lee Creek Mine, Aurora, N.C. (1958-2007). Virginia Museum of Natural History, Special Publication 14, pp. 325–432.

Research Note

New and confirmed fish hosts for the threatened freshwater mussel *Lampsilis bracteata* (Gould, 1855), the Texas Fatmucket (Bivalvia: Unionidae)

The widespread decline of the freshwater mussel fauna endemic to Texas indicates fundamental changes to the ecology of the river systems inhabited by these species. In order to appropriately manage these declining species, it is imperative to understand their life history characteristics. *Lampsilis bracteata* (Gould, 1855) has experienced a precipitous decline in recent decades (Howells, 2010). Historically, the species was dispersed throughout the headwaters of the Edwards Plateau region and was found in the Colorado and Guadalupe–San Antonio drainages (Howells, 2010). However, as only several small populations are currently known to exist within these basins, the species is listed as state threatened by the Texas Parks and Wildlife Department (Texas Register 35, 2010) and as a candidate species for federal protection by the U.S. Fish and Wildlife Service (USFWS) (USFWS, 2011).

The purpose of this study was to confirm previously identified host fishes (Howells, 1997) and identify additional hosts on which *L. bracteata* glochidia may successfully transform. Although the reproductive biology of this species has been studied to some degree in the past (Howells, 1997), the quality of glochidia transformation on previously identified host fishes and their suitability for large-scale artificial propagation efforts remain unknown.

Two trials of glochidial infestations were performed on potential hosts, including *Lepomis cyanellus* (Rafinesque, 1819), *Lepomis macrochirus* (Rafinesque, 1819), *Micropterus salmoides* (Lacépède, 1802), and *Micropterus treculii* (Vaillant and Bocourt, 1883) (Table 1). Our methods followed standard host-identification protocols (Jones et al., 2004) and utilized a passive infestation technique. Each trial was conducted independently using new batches of fish and glochidia from different females. At the time of the study, the only fish available were species already housed at the USFWS San Marcos National Fish Hatchery and Technology Center (Table 1).

Displaying gravid *L. bracteata* females were observed in the San Saba River in Menard County, Texas, between July and October 2011. Females were found by searching bedrock crevices in the river bottom while diving with the aid of a mask and snorkel. We checked displaying females for gravidity by carefully opening the valves and inspecting for inflated marsupial gills. Glochidia were collected from gravid mussels in July of 2011 by flushing well water through the marsupial gills using a hypodermic needle. Potential host fishes were placed in a plastic container holding 7.5 L of water. Glochidia from two females also were placed in the container. Airstones were used to agitate the water in the container for 45 min. After infestation, fish were separated by species and placed in individual aquaria. We performed infestations on the same days that glochidia were collected. Shell length, height, and hinge length were measured for glochidia and newly transformed juveniles (to the nearest 0.01 mm). Infested fish were maintained in aquaria between 21 and 24 °C, which were siphoned every 2 d for the first 14 d of the trial and daily thereafter. We counted the total number of juvenile mussels produced per fish (Table 1).

We were able to successfully transform a moderate to high number of glochidia on all four of the tested fish species. We confirmed two previously identified hosts and identified two new hosts (Table 1). Transformation time among the four fish species ranged from 17 to 26 d. *Lepomis cyanellus* produced the greatest number of juveniles per fish (Table 1). Glochidia of *L. bracteata* had a mean height of 0.21 mm, mean length of 0.18 mm, and mean hinge length of 0.10 (SE < 0.01 and $n = 10$). Glochidia grew only slightly during transformation on the hosts. Newly transformed juveniles had a mean height of 0.25 mm, mean length of 0.22 mm, and mean hinge length of 0.10 mm (SE < 0.01 and $n = 10$).

The use of a mantle flap lure (Figure 1) and centrarchid hosts by *Lampsilis bracteata* parallels what researchers have recorded for other *Lampsilis* spp. throughout the United States (Zale and Neves, 1982, Haag et al., 1999). The successful transformation of *L. bracteata* on fish species that are readily available to state and federal fish hatcheries is

Table 1. Results of fish host trials for *Lampsilis bracteata* conducted in 2011. (*) previously identified by Howells (1997)

	Number Tested		Days to Transformation		Mean number of juveniles per fish	
	Trials		Trials		Trials	
Fish Species	1	2	1	2	1	2
*Lepomis cyanellus**	5	5	24	18	434	129
*Lepomis macrochirus**	-	6	-	17	-	95
Micropterus salmoides	-	5	-	26	-	69
Micropterus treculii	-	10	-	26	-	60

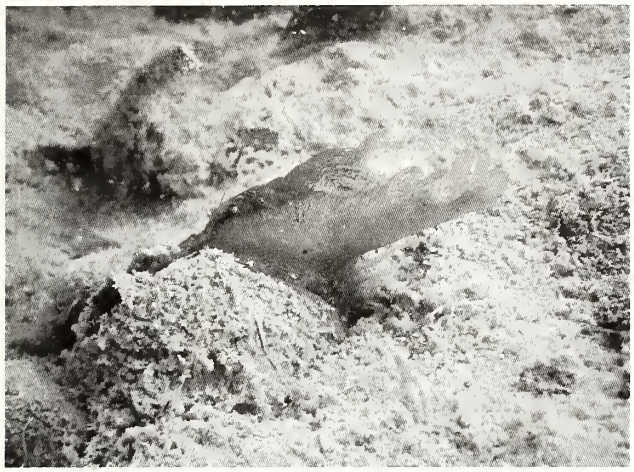

Figure 1. Mantle display of a gravid female *Lampsilis bracteata* observed in the San Saba River, Menard Co., Texas on July 22, 2011.

promising for future artificial propagation. Furthermore, the successful propagation and advancement of juvenile grow-out procedures for other *Lampsilis* spp. provides a guide for the production of juveniles that may be used to augment wild populations or reintroduce the species into areas where it has been extirpated. Although such a strategy has already been developed, researchers within Texas still need to invest time and resources into elucidating the details of this species' life history and ecological requirements.

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LITERATURE CITED

Haag, W.R., M.L. Warren Jr., and M. Shillingsford. 1999. Host fishes and host-attracting behavior of *Lampsilis altilis* and *Villosa vibex* (Bivalvia: Unionidae). American Midland Naturalist 141:149–157.

Howells, R.G. 1997. New fish hosts for nine freshwater mussels (Bivalvia: Unionidae) in Texas. Texas Journal of Science 49: 255–258.

Howells, R.G. 2010. Rare mussels: Summary of selected biological and ecological data for Texas. Report submitted to U.S. Fish & Wildlife. Report on file with Save Our Springs Alliance.

Jones, J.W., R.J. Neves, S.A. Ahlstedt, and R.A. Mair. 2004. Life history and propagation of the endangered dromedary pearlymussel (*Dromus dromas*) (Bivalvia: Unionidae). Journal of the North American Benthological Society 23: 515–525.

Texas Register 35. 2010. Threatened and endangered nongame species. Chapter 65. Wildlife Subchapter G. 31 TAC §65.175. Adopted rules. January 8, 2010. 249-251. Texas Secretary of State.

U.S. Fish and Wildlife Service (USFWS). 2011. Endangered and threatened wildlife and plants: 90-day finding on petitions to list nine species of mussels from Texas as threatened or endangered with critical habitat. Federal Register 74: 66260–66271.

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Taxonomic review of Triphorinae (Gastropoda: Triphoridae) from the Vitória-Trindade Seamount Chain, southeastern Brazil

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ABSTRACT

In the present work we identified the shells of Triphorinae collected at the seamounts of the Vitória-Trindade Chain off southeastern Brazil by the expeditions MD55 and REVIZEE-Central, the main sources of mollusks from the study site in the last decades. Of the 13 species found in this study, *Cosmotriphora melanura* and *Nototriphora decorata* were previously reported from the Vitória-Trindade Chain. *Cosmotriphora arnoldoi*, *Iniforis carmelae*, *Iniforis pseudothomae*, *Latitriphora albida*, *Coriophora novem*, *Triphora ellyae* and *Triphora elvirae* are reported for the first time from Brazil. The known ranges in Brazil of *Monophorus olivaceus* and *Triphora atlantica* are extended to the Vitória-Trindade Chain. *Isotriphora tigrina* new species, diagnosed by its teleoconch with two main spiral cords and three brown and smooth basal cords, is currently restricted to the Vitória-Trindade Chain and Bahia state. *Isotriphora onca* new species, diagnosed by its teleoconch with two main spiral cords and creamy to light brown color, is currently restricted to the Vitória-Trindade Chain. The number of species of Recent Triphoridae in the Vitória-Trindade Chain increased from six to 15, and in Brazil from 17 to 26.

Additional Keywords: Western Atlantic, MD55, REVIZEE, Mollusca, Triphoroidea, RV Marion-Dufresne

INTRODUCTION

Triphoridae is a large group of marine microgastropods that feed on sponges, mainly distributed in tropical and temperate seas (Marshall, 1983). Triphorids are usually recognized by their left-coiled shell, although species of Metaxiinae are dextral. Bouchet and Rocroi (2005) considered the existence of three subfamilies: Triphorinae, Metaxiinae, and Iniforinae, although the validity of the latter is contested by Marshall (1983). We follow Nützel (1998), recognizing only Triphorinae and Metaxiinae.

The maximum diversity of Triphoridae is found in the tropical Indo-Pacific (Rolán and Fernández-Garcés, 2008). In the western Atlantic, there are 93 recent species (Simone, 2006; Rolán and Fernández-Garcés, 2008, 2009; Faber, 2010; Fernandes and Pimenta, 2011). In Brazil, 17 species are reported (Absalão, 1989; Simone, 2006; Rolán and Fernández-Garcés, 2008; Lee, 2009; Rios, 2009; Fernandes and Pimenta, 2011), although some of them need confirmation.

The Vitória-Trindade Seamount Chain (Vitória-Trindade Ridge; Columbia Fracture Zone) comprises a series of seamounts and oceanic islands between 20°–21° S and 28°50′ – 38°30′ W, off Espírito Santo state, southeastern Brazil. The sequence of seamounts initiates near the base of the continental slope (Champlain and Vitória seamounts), running eastward to Trindade Island and Martin Vaz Archipelago (Figure 1), about 1167 km from the continent (Leal, 1991; O'Hara et al., 2010). Only Trindade Island and Martin Vaz Archipelago rise above sea level, while the seamount summits rise to between 50 and 150 m below the surface. The Vitória-Trindade Chain is under the influence of the warm, saline, southward-flowing Brazil Current (O'Hara et al., 2010).

Two scientific expeditions provided the majority of mollusks collected at the Vitória-Trindade Chain in the last decades: the French-Brazilian Expedition MD55, conducted in 1987, and REVIZEE-Central ("Programa de Avaliação do Potencial Sustentável de Recursos Vivos da Zona Econômica Exclusiva", SCORE Central; "Program of Evaluation of the Sustainable Potential of Living Resources in the Exclusive Economic Zone", SCORE Central), conducted between 1996 and 2002.

The prosobranchs collected at the Vitória-Trindade Chain by the Expedition MD55 were studied by Leal (1991) as the basis for a biogeographic analysis of the oceanic islands of Brazil. Leal (1991) recognized 10 taxa

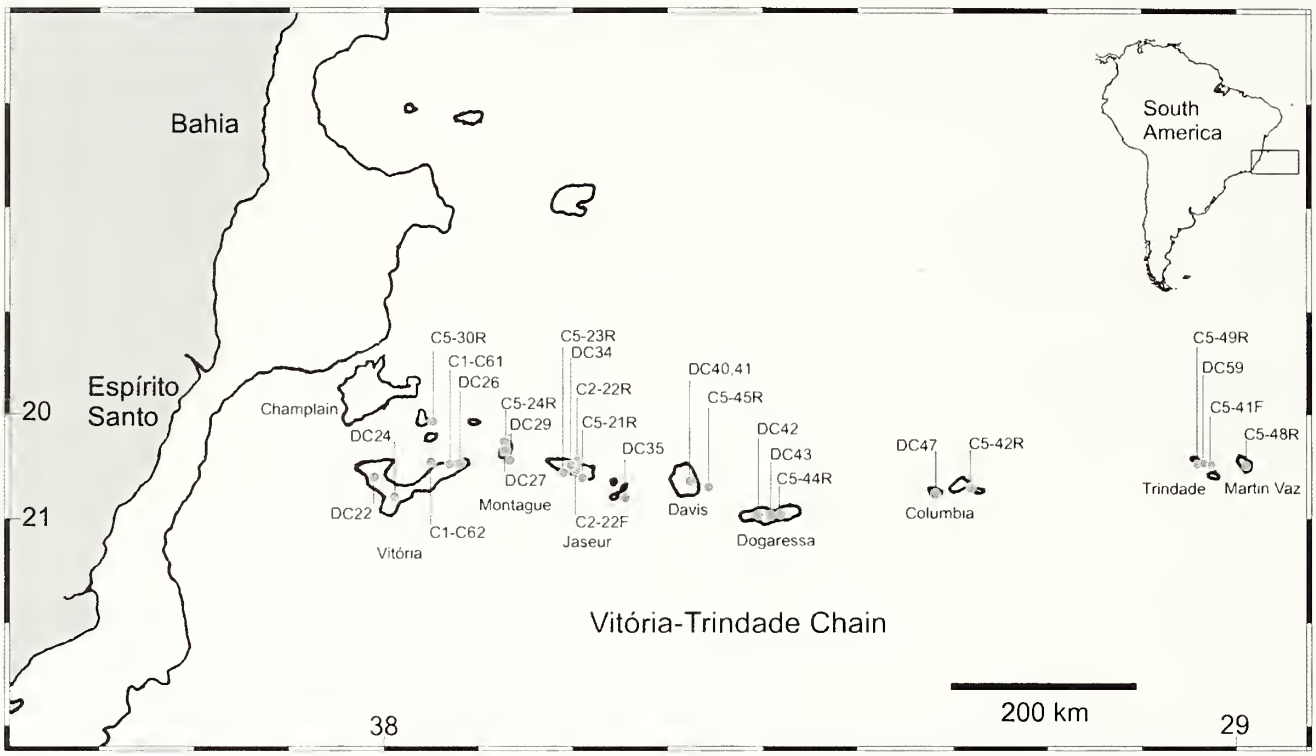


Figure 1. Stations in which shells of Triphoridae were collected at the Vitória-Trindade Chain by Expedition MD55 (DC) and REVIZEE-Central (C1–C5).

for Triphoridae, of which seven were identified only at generic level, although that author admitted that "some of the study species do not fit these classifications at the generic level". Absalão et al. (2006) listed six species of triphorids from the Vitória-Trindade Chain, collected by REVIZEE. Fernandes and Pimenta (2011) reported *Metaxia excelsa* Faber and Moolenbeek, 1991 and *Metaxia prompta* Rolán and Fernández-Garcés, 2008 at the study site.

Within these works, the species reported at the Vitória-Trindade Chain are *Metaxia excelsa*, *Metaxia prompta*, *Cosmotriphora melanura* (C. B. Adams, 1850), *Nototriphora decorata* (C. B. Adams, 1850), *Iniforis turristhomae* (Holten, 1802) and *Marshallora nigrocincta* (C. B. Adams, 1839) in addition to seven morphotypes that remained identified only at generic level.

As the Metaxiinae were already revised for Brazil (Fernandes and Pimenta, 2011), the present work is focused on the taxonomy of Triphorinae from the Vitória-Trindade Chain based on the material collected by the expeditions MD55 and REVIZEE-Central.

MATERIALS AND METHODS

In May/June 1987, the Research Vessel Marion-Dufresne made a series of dredgings and trawlings in southern Bahia state (Abrolhos bank) and in the Southeast region of Brazil, during the Expedition MD55 (Tavares, 1999). There were 66 benthic collecting stations, in depths between 15 and 5100 m, including the top of the seamounts that form the Vitória-Trindade Chain. The stations in which shells of Triphoridae were collected at the Vitória-Trindade Chain by the Expedition MD55 are listed in Table 1.

The program REVIZEE was divided in four regions (one for each SCORE), representing the different oceanographic characteristics of the Brazilian coast (Lavrado, 2006). The SCORE Central comprised the area between Salvador (Bahia state) to Cabo de São Tomé (Rio de Janeiro state), including the Vitória-Trindade Chain. REVIZEE-Central consisted of six campaigns (C1 to C6), of which the first one (C1) was conducted by the Oceanographic Ship Antares and the remainder (C2 to C6) by the supply boat N/RB Astro Garoupa. There were 227 collecting stations, in depths between 12 to 2076 m. The stations in which shells of Triphoridae were collected at the Vitória-Trindade Chain by REVIZEE-Central are listed in Table 2.

All material available consisted of empty shells. The taxonomic identifications were based on conchological comparisons under a stereomicroscope. Each species was also observed in scanning electron microscope (SEM) images. The whorl-counting procedure follows Leal (1991). The embryonic shell is here considered the beginning of the protoconch, typically sculptured on Triphorinae with spherical granules, cruciform granules or reticulated pattern. The remainder whorls of the protoconch constitute the larval shell, usually sculptured on Triphorinae with spiral and axial cords.

Table 1. Stations at the Vitória-Trindade Chain yielding Triphoridae shells during the Cruise MD55. DC: Charcot dredge.

Locality	Station	Date	Latitude S	Longitude W	Depth (m)
Vitória	9-DC22	13/v/1987	20°32′	38°11′	52
	10-DC24	13/v/1987	20°42′	37°50′	48–52
	13-DC26	14/v/1987	20°21′	36°59′	97
Montague	14-DC27	14/v/1987	20°26′	36°42′	81
	16-DC29	14/v/1987	20°27′	36°41′	310–350
Jaseur	20-DC34	15/v/1987	20°28′	35°54′	54
	21-DC35	16/v/1987	20°42′	35°22′	82–105
Davis	23-DC40	17/v/1987	20°40′	34°41′	60
	23-DC41	17/v/1987	20°39′	34°43′	58–70
Dogaressa	24-DC42	17/v/1987	20°55′	34°01′	60
	25-DC43	17/v/1987	20°51′	33°45′	63
Columbia	27-DC47	19/v/1987	20°42′	32°13′	94–105
Trindade	35-DC59	22/v/1987	20°30′	29°19′	52–60

Table 2. Stations at the Vitória-Trindade Chain yielding Triphoridae shells during REVIZEE-Central.

Locality	Station	Date	Latitude S	Longitude W	Depth (m)
Champlain	C5-30R	13/vii/2001	20°09′	37°29′	60
Vitória	C1-C61	24/iv/1996	20°31′	37°19′	88
	C1-C62	25/iv/1996	20°30′	37°28′	96
Montague	C5-24R	13/vii/2001	20°21′	36°38′	55
Jaseur	C2-22F	08/xi/1997	20°36′	35°52′	110
	C2-22R	08/xi/1997	20°31′	35°50′	59
	C5-21R	12/vii/2001	20°42′	35°42′	57,5
	C5-23R	12/vii/2001	20°29′	36°06′	55
Davis	C5-45R	12/vii/2001	20°41′	34°35′	108
Dogaressa	C5-44R	11/vii/2001	20°51′	33°38′	65
Columbia	C5-42R	11/vii/2001	20°44′	31°50′	85
Trindade	C5-41F	10/vii/2001	20°30′	29°16′	360
	C5-49R	10/vii/2001	20°31	29°21′	57
Martin Vaz	C5-48R	10/vii/2001	20°29′	28°51′	52

In order to obtain complete sinonimic lists, some citations were included even without direct or indirect examination of the respectively material. In these cases, the expression "not illustrated" follows the citation.

In the section of "material examined", the number inside brackets indicates the quantity of shells in each lot.

Abbreviations used: (ABC Islands) Aruba, Bonaire and Curaçao; (AMNH) American Museum of Natural History, New York, USA; (ANSP) Academy of Natural Sciences, Philadelphia, USA; (CER) E. Rolán, Vigo, Spain; (CFG) R. Fernández-Garcés, Cienfuegos, Cuba; (FLMNH) Florida Museum of Natural History, Gainesville, USA; (IBUFRJ) Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; (IES) Instituto de Ecología y Sistemática, Havana, Cuba; (MCZ) Museum of Comparative Zoology, Cambridge, USA; (MHNS) Museo de Historia Natural, Santiago de Compostela, Spain; (MNCN) Museo Nacional de Ciencias Naturales, Madrid, Spain; (MNHN) Muséum national d'Histoire naturelle, Paris, France; (MNRJ) Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; (MORG) Museu Oceanográfico do Rio Grande, Rio Grande, Brazil; (MZSP) Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; (NHM) Natural History Museum, London, England; (ZMA) Zoologisch Museum Amsterdam, Amsterdam, The Netherlands.

RESULTS

Family Triphoridae Gray, 1847
Subfamily Triphorinae Gray, 1847

Diagnosis: Sinistral shells, with a tubular or subtubular anterior canal, the posterior canal forming a notch, a hole or a tube (based on Wilson, 1993).

Genus *Cosmotriphora* Olsson and Harbison, 1953

Type Species: *Cerithium melanura* C. B. Adams, 1850, original designation; Recent, Atlantic Ocean.

Diagnosis: Embryonic shell with granules on abapical region, larval shell with axial riblets crossed by one spiral cord at beginning, two cords latter; teleoconch with a later development of median spiral cord; radular formula 9-1-1-1-9, with four cusps on central and lateral teeth,

three cusps on internal marginal teeth, two cusps on external marginal teeth (based on the description of the type species of the genus in Bouchet, 1985).

***Cosmotriphora arnoldoi* Faber and Moolenbeek, 1991**
(Figures 2, 18, 29)

Cosmotriphora arnoldoi Faber and Moolenbeek (1991: 81, figs. 1–2); Rolán and Fernández-Garcés (1994: 20, figs. 12–15; 2007: 20, pl. I, figs. 19–21); Lee (2009: 88, text-fig.); Garcia and Lee (2011).
Triphora melanura: Absalão et al. (2006: 238, in part) non C. B. Adams, 1850.
Triphora sp.: Absalão et al. (2006: 238, in part).

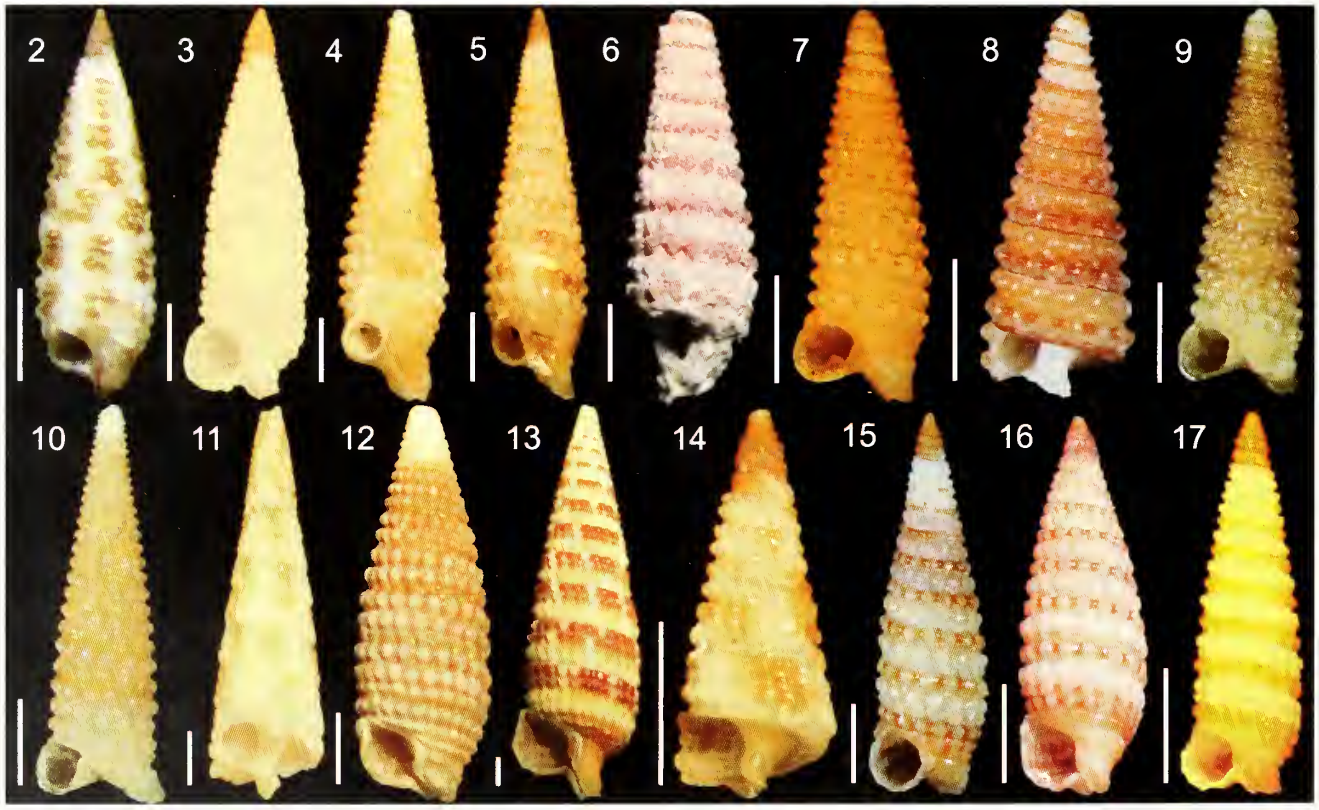
Type Material: Holotype: ZMA 391001. One paratype ZMA 391002.

Type Locality: Playa Lechi, Bonaire.

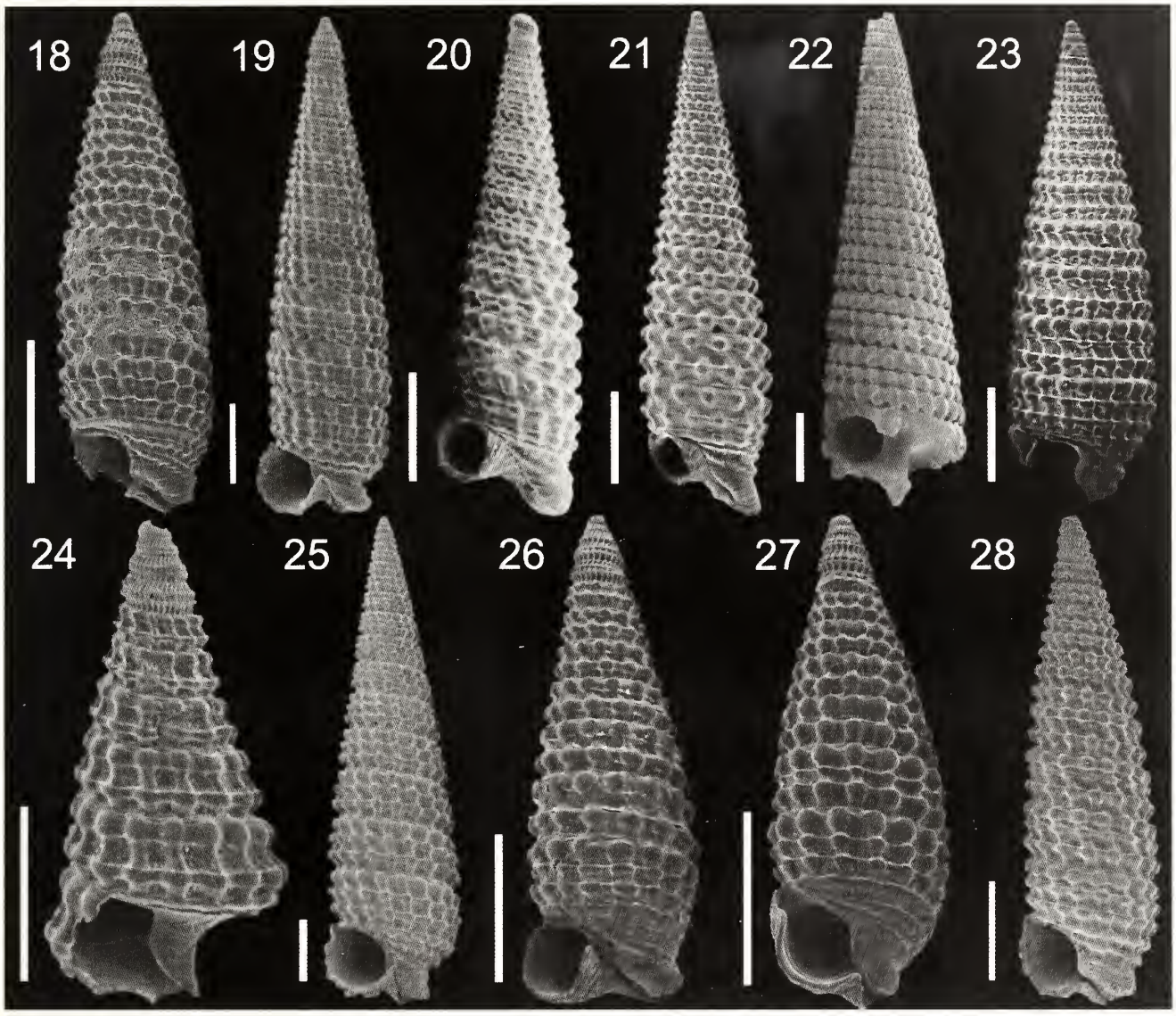
Material Examined: IBUFRJ 13568, REVIZEE C5-24R [1]; IBUFRJ 19447, REVIZEE C1-C62 [2]; MORG 51900, REVIZEE C1-C62 [3]; MNHN, MD55 35-DC59 [1].

Remarks: In addition to *C. arnoldoi*, the other species of *Cosmotriphora* in the West Atlantic is *C. melanura* (C. B. Adams), which has an earlier development of the median spiral cord (Figure 19) and a white teleoconch (Figure 3), instead of the reddish-brown blotches in the teleoconch of *C. arnoldoi* (Figure 2). This pattern of coloration is similar to *Nototriphora decorata* (C. B. Adams, 1850), a very common species in the West Atlantic. *Cosmotriphora arnoldoi* has a more curvilinear profile; its median spiral cord of the teleoconch has the same size as the adapical and abapical spiral cords on the eighth/ninth whorl (although appearing weakly on the fifth whorl) (Figure 18), while in *N. decorata* it reaches the same size on the fifth/sixth whorl (Figure 25); its axial blotches are more or less parallel, not irregular as in *N. decorata*; the three spiral cords are covered by blotches, except in the body whorl, where the adapical spiral cord is usually totally white (Figure 2).

The generic placement of this species by Faber and Moolenbeek (1991) was made without knowledge of radula and operculum, possibly only using protoconch morphology (Rolán and Fernández-Garcés, 1994). The presence of granules on the entire embryonic whorl of



Figures 2–17. Triphoridae species. **2.** *Cosmotriphora arnoldoi*, MNHN. **3.** *Cosmotriphora melanura*, MNRJ 25019. **4.** *Iniforis carinelae*, MNRJ 25014. 5. *Iniforis pseudothomae*, MNRJ 25033. **6.** *Iniforis* sp., IBUFRJ 10563. **7.** *Isotriphora tigrina* new species, MNRJ 25992, holotype. **8.** *Isotriphora tigrina* new species, MNRJ 16227, paratype. **9.** *Isotriphora onca* new species, MNRJ 16236, holotype. **10.** *Isotriphora onca* new species, MNHN IM-2012-2111, paratype. **11.** *Latitriphora albida*, MNRJ 25016. **12.** *Coriophora novem*, MNRJ 25008. **13.** *Monophorus olivaceus*, MNRJ 25027. **14.** *Nototriphora decorata*, MNRJ 25002. **15.** *Triphora atlantica*, IBUFRJ 13142. **16.** *Triphora ellyae*, MNRJ 18955. **17.** *Triphora elvirae*, MNHN. Scale bar = 1 mm.



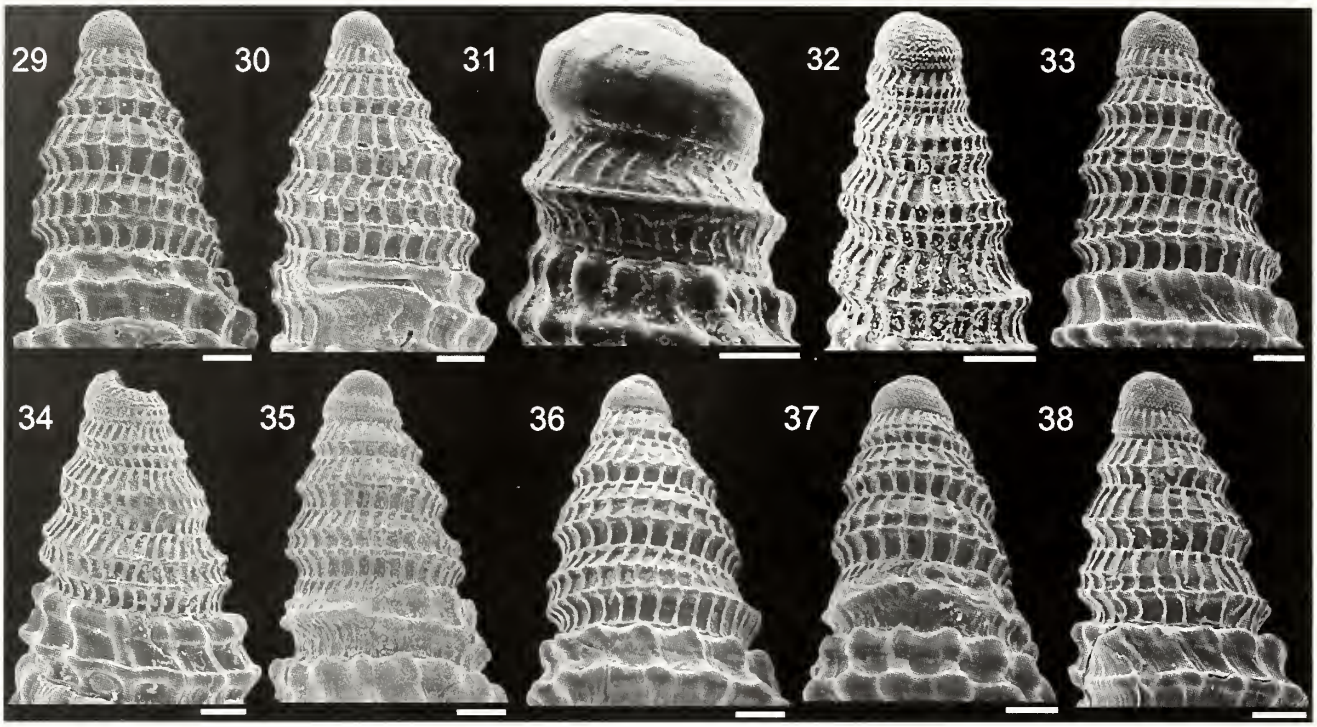
Figures 18–28. Triphoridae species. **18.** *Cosmotriphora arnoldoi*, IBUFRJ 13568. **19.** *Cosmotriphora melanura*, MNRJ 25024. **20.** *Iniforis carnelae*, MNRJ 25541. **21.** *Iniforis pseudothomae*, MNRJ 25033. **22.** *Latitriphora albida*, MNRJ 25016. **23.** *Coriophora novem*, MNRJ 25011. **24.** *Monophorus olivaceus*, MNHN. **25.** *Nototriphora decorata*, MNRJ 25033. **26.** *Triphora atlantica*, IBUFRJ 13142. **27.** *Triphora ellya*e, MNRJ 18955. **28.** *Triphora elvirae*, MNRJ 25032. Scale bar = 1 mm.

C. arnoldoi (Figure 29), not only on its abapical region as in *C. melanura* (Figure 30), suggests an affinity with the genus *Nototriphora* Marshall, 1983, pending confirmation about the importance of this difference between *Cosmotriphora* and *Nototriphora*. Marshall (1983) mentioned only differences in operculum and radula about the two genera.

Distribution: USA: Florida (Lee, 2009), Louisiana (Garcia and Lee, 2002); Gulf of Mexico (Rosenberg et al., 2009); Bahamas (Faber and Moolenbeek, 1991); Cuba (Rolán and Fernández-Garcés, 1994); Puerto Rico (Faber and Moolenbeek, 1991); ABC Islands (type locality); Brazil: Vitória-Trindade Chain (this study).

***Cosmotriphora melanura* (C. B. Adams, 1850)**
(Figures 3, 19, 30)

Cerithium melanura C. B. Adams (1850: 117); Clench and Turner (1950: 307, pl. 38, fig. 10).
Triforis melanura: Dall and Simpson (1901: 423, pl. 58, fig. 7).
Triforis grimaldii Dautzenberg and Fischer (1906: 41, pl. III, figs. 9–10).
Triphora melanura: Rios (1970: 45, not illustrated; 1975: 50, pl. 13, fig. 187; 1985: 161, pl. 53, fig. 761; 1994: 94, pl. 31, fig. 374; 2009: 172, text-fig.); Abbott (1974: 111, fig. 1134); Vokes and Vokes (1983: 18, pl. 27, fig. 14); Jong and Coomans (1988: 49, not illustrated); Absalão



Figures 29–38. Protoconchs. **29.** *Cosmotriphora arnoldoi*, IBUFRJ 13568. **30.** *Cosmotriphora melanura*, MNRJ 25024. **31.** *Iniforis carnelae*, MNRJ 25541. **32.** *Iniforis pseudothomae*, MNRJ 25033. **33.** *Coriophora novem*, MNHN. **34.** *Monophorus olivaceus*, MNHN. **35.** *Nototriphora decorata*, MNRJ 25033. **36.** *Triphora atlantica*, IBUFRJ 13142. **37.** *Triphora ellyae*, MNRJ 18955. **38.** *Triphora elvirae*, MNHN. Scale bar = 100 µm.

(1989: 3, not illustrated); Merlano and Hegedus (1994: 148, pl. XLVI, fig. 524); Absalão et al. (2006: 238, fig. 9, in part); Gomes et al. (2006: 188,not illustrated); Santos et al. (2007: 226, not illustrated).

Cosmotriphora melanura: Marshall (1983: 110, fig. 27 D-F); Bouchet (1985: 35–37, fig. 27); Fernandes and Rolán (1988: 22, pl. 1, fig. 1, pl. 2, fig. 2); Leal (1991: 120, pl. 16, figs. F-G); Rolán and Fernández-Garcés (1994: 19, figs. 11, 25, 26, 30 CM); Redfern (2001: 65, pl. 32, fig. 274); Espinosa and Ortea (2001: 20, not illustrated); Ardovini and Cossignani (2004: 134, text-fig.); Rolán (2005: 106, pl. 30, fig. 438); Rolán and Fernández-Garcés (2007: 20, pl. 1, figs. 14–16); Jensen and Pearce (2009: 128, not illustrated); Lee (2009: 88, text-fig.); Tunnell et al. (2010: 204, text-fig.); Garcia and Lee (2011).

Triphora (Cosmotriphora) melanura: Odé (1989: 109, fig. 3).

Triphora sp.: Absalão et al. (2006: 238, in part).

Type Material: Lectotype: MCZ 186159.

Type Locality: Jamaica.

Material Examined: IBUFRJ 9309, REVIZEE C1-C61 [52]; IBUFRJ 10222, REVIZEE C1-C62 [11]; IBUFRJ 11952, REVIZEE C5-23R [1]; IBUFRJ 11993, REVIZEE C5-42R [1]; IBUFRJ 12010, REVIZEE C5-45R [1]; IBUFRJ 12018, REVIZEE C5-48R [1]; IBUFRJ 13567, REVIZEE C5-24R [5]; IBUFRJ 13581, REVIZEE C5-23R [6]; IBUFRJ 13594, REVIZEE C5-45R [3]; IBUFRJ 13749, REVIZEE C5-24R [8]; IBUFRJ 14372, REVIZEE C5-45R [1]; IBUFRJ 14577, REVIZEE C5-30R [6]; IBUFRJ 14649, REVIZEE C5-49R [2]; IBUFRJ 14674, REVIZEE C5-44R [14]; IBUFRJ 14694, REVIZEE C5-48R [3]; IBUFRJ 14713, REVIZEE C5-45R [2]; IBUFRJ 14717, REVIZEE C5-42R [3]; IBUFRJ 19457, REVIZEE C1-C61 [14]; IBUFRJ 19458, REVIZEE C1-C62 [8]; MNRJ 12740, REVIZEE C5-42R [5]; MNRJ 12768, REVIZEE C5-21R [1]; MNRJ 25017, MD55 24-DC42 [3]; MNRJ 25018, MD55 23-DC41 [5]; MNRJ 25019, MD55 25-DC43 [5]; MNRJ 25020, MD55 10-DC24 [3]; MNRJ 25021, MD55 14-DC27 [1]; MNRJ 25022, MD55 21-DC35 [28]; MNRJ 25023, MD55 23-DC40 [1]; MNRJ 25024, MD55 9-DC22 [6]; MORG 51899, REVIZEE C1-C62 [3]; MNHN, MD55 20-DC34 [23]; MNHN, MD55 25-DC43 [3]; MNHN, Enseada dos Portugueses, Trindade Is., v/1987 [2].

Remarks: This species is clearly distinguished by its white teleoconch and brown protoconch (Figure 3), with a mammilliform shape (Figure 30). This was by far the most common species on the material studied, and it has an amphi-Atlantic distribution (Rolán and Fernández-Garcés, 1994). However, the shells of *C. melanura* of the East Atlantic seem to have some differences with the Caribbean shells, especially the later development of the median spiral cord in the teleoconch (Bouchet, 1985). In the material examined by Bouchet (1985) and

Rolán and Fernández-Garcés (1994) of the west coast of Africa, the median spiral cord appears between the sixth and eighth whorl, while in the shells herein studied and the Caribbean ones (e.g., Rolán and Fernández-Garcés, 1994) this cord usually begins in the third whorl (Figure 19). Following Rolán and Fernández-Garcés (1994), the protoconchs and radulae of the two populations seem to be similar, and we accept the small divergence in the development of the median spiral cord as an intraspecific variation. This morph is the basis for the well-established synonym *Triforis grimaldii* Dautzenberg and Fischer, 1906, from the west coast of Africa.

Triphora dealbata (C. B. Adams, 1850), from Jamaica, is considered by some authors (e.g. Rolán and Fernández-Garcés, 2008) as a possible synonym for *C. melanura*.

In addition to a wide geographic distribution, *Cosmotriphora melanura* is also considered by Dall (1892) to be present in the Miocene of Florida.

Distribution: Europe (Bouchet, 1985); West coast of Africa (Rolán, 2005); Bermuda (Jensen and Pearce, 2009); USA: North Carolina (Abbott, 1974), Florida (Lee, 2009), Louisiana (Garcia and Lee, 2002), Texas (Tunnell et al., 2010); Mexico (Vokes and Vokes, 1983); Bahamas (Redfern, 2001); Cuba (Rolán and Fernández-Garcés, 1994); Belize (Miloslavich et al., 2010); Jamaica (type locality); Puerto Rico (Dall and Simpson, 1901); Virgin Islands; Costa Rica (Espinosa and Ortea, 2001); Colombia (Merlano and Hegedus, 1994); ABC Islands (Jong and Coomans, 1988); Brazil: Amapá to Bahia (Rios, 1985), São Pedro-São Paulo Is. (Rios, 2009), Fernando de Noronha and Vitória-Trindade Chain (Leal, 1991; Gomes et al., 2006), Espírito Santo (Absalão, 1989; Absalão et al., 2006), Rio de Janeiro (Absalão, 1989; Absalão et al., 2006; Santos et al., 2007).

Genus *Iniforis* Jousseaume, 1884

Type Species: *Iniforis malvaceus* Jousseaume, 1884, original designation; Recent, New Caledonia.

Diagnosis: Paucispiral or multispiral protoconch; teleoconch whorls with two rows of large nodules and granulose interspaces; suture indistinguishable; aperture round; posterior and anterior canals short and tubular (based on Wilson, 1993).

Iniforis carmelae Rolán and Fernández-Garcés, 1993

(Figures 4, 20, 31)

Triphora sp. 3: Leal (1991: 123, pl. 17, figs. A–B).
Iniforis carmelae Rolán and Fernández-Garcés (1993: 102, figs. 12–15, 28–30; 2007: 21, pl. II, figs. 18–22).

Type Material: Holotype: MNCN 15.05/6822. Paratypes: One in ZMA 3.93.006, AMNH 226457, IES, NHM 1992134, MNHN; five in the CFG; 15 in the CER.

Type Locality: Cienfuegos, in the South of Cuba.

Material Examined: MNRJ 25013, MD55 35-DC59 [2]; MNRJ 25014, MD55 21-DC35 [1]; MNRJ 25541, MD55 9-DC22 [1].

Remarks: The material here studied agrees with the original description in having the white and relatively broad protoconch with approximately 2.75 whorls (Figure 31) and the later development of a very small median spiral cord on the teleoconch (ninth/tenth whorl, very close to the adapical spiral cord; Figure 20) in addition to the discontinuous brown coloration on the abapical spiral cord of the teleoconch (Figure 4). However, the shells from Vitória-Trindade Chain display some slight differences from the original description: a more tuberculated subperipheral cord (Figure 20, if compared to the figure 28 in Rolán and Fernández-Garcés, 1993), the continuous brown coloration of the abapical spiral cord of the teleoconch on its initial whorls (Figure 4), and the spiral cord on the second whorl of the protoconch is positioned in its middle (Figure 31) although the original description shows this spiral cord situated barely under the middle of the whorl (figs. 29–30 in Rolán and Fernández-Garcés, 1993).

Iniforis carmelae can be best differentiated from *Iniforis immaculata* Rolán and Fernández-Garcés, 1993, a species from Cuba, by the shell color, translucent white in the later. *Iniforis gudeliae* Rolán and Fernández-Garcés, 2009 and *Iniforis pelorcei* Rolán and Fernández-Garcés, 2009, two species from the Caribbean, have the second whorl of protoconch with two spiral cords (*I. carmelae* has only one) in addition to a more continuous brown coloration on the abapical spiral cord of the teleoconch.

Distribution: Gulf of Mexico (Rosenberg et al., 2009); Cuba (type locality); Brazil: Vitória-Trindade Chain (this study).

Iniforis pseudothomae Rolán and Fernández-Garcés, 1993

(Figures 5, 21, 32)

Triphora sp. 2: Leal (1991: 123, pl. 16, figs. L–M).
Iniforis pseudothomae Rolán and Fernández-Garcés (1993: 100, figs. 5–8, 22–23; 2007: 21, pl. II, figs. 9–12).
Triphora decorata: Absalão et al. (2006: 238, in part) non C. B. Adams, 1850.
Triphora melanura: Absalão et al. (2006: 238, in part) non C. B. Adams, 1850.
Triphora sp.: Absalão et al. (2006: 238, in part).
Triphora turristhomae: Rios (2009: 173, text-fig.) non Holten, 1802.

Type Material: Holotype: MNCN 15.05/6820. Paratypes: One in AMNH 226459, MNHN, NHM 1992133, ZMA 3.93.005; five in the IES; ten in the CER and CFG.

Type Locality: Cienfuegos, in the South of Cuba.

Material Examined: IBUFRJ 19443, REVIZEE C5-30R [1]; IBUFRJ 19455, REVIZEE C1-C61 [1]; MNRJ 25033, MD55 9-DC22 [8]; MNRJ 25034, MD55 25-DC43 [2]; MNHN, MD55 20-DC34 [4].

Remarks: As suspected by Rolán and Fernández-Garcés (1993), *Triphora* sp. 2 in Leal (1991) represents *Iniforis pseudothomae*. This species has a teleoconch very similar to *I. carmelae*, with discontinuous brown color on the abapical spiral cord (Figure 5); shells of *I. pseudothomae* never develop a median spiral cord as *I. carmelae*. Also, the brown and elongated protoconch of *I. pseudothomae* has around 5–5.5 whorls and two spiral cords on the larval shell, except on the last whorl (Figure 32), instead of the ~2.75 white whorls of *I. carmelae*, with one spiral cord on the larval shell (Figure 31). The brown and mutispiral protoconch of *I. pseudothomae* also differentiates it from *I. gudeliae* and *I. pelorcei*.

The illustration provided by Rios (2009) as *Triphora turristhomae* (Holten, 1802) actually depicts *I. pseudothomae*. Possibly the records of *Iniforis turristhomae* (Holten, 1802) from Brazil are erroneous (Leal, 1991), and they can be actually referred to *I. pseudothomae*, but this hypothesis demands further investigation. *Iniforis turristhomae* has a continuous brown band on the abapical spiral cord of the teleoconch and two spiral cords on the protoconch in contrast to *I. pseudothomae*, which has a discontinuous brown band on the abapical spiral cord of the teleoconch (Figure 5) and only one spiral cord on the last whorl of the protoconch (Figure 32).

The single shell of *Iniforis turristhomae* (Holten, 1802) from the Vitória-Trindade Chain, reported by Absalão et al. (2006) (IBUFRJ 10563, station REVIZEE C2-22F), is very eroded, making a correct identification difficult. Actually, this shell has a continuous brown band on the abapical spiral cord (Figure 6), ruling out *I. pseudothomae*. The presence of brown color between the two spiral cords and the development of a very small median cord on the body whorl adjacent to the adapical spiral cord are not consistent with *I. turristhomae*. We prefer to maintain this shell as *Iniforis* sp., invalidating the previous record of *I. turristhomae* for the Vitória-Trindade Chain.

Distribution: Gulf of Mexico (Rosenberg et al., 2009); Cuba (type locality); ABC Islands (Miloslavich et al., 2010); Brazil: Vitória-Trindade Chain (this study).

Genus *Isotriphora* Cotton and Godfrey, 1931

Type Species: *Triforis tasmanica* Tenison-Woods, 1875, original designation; Recent, southern Australia.

Diagnosis: Paucispiral protoconch, blunt-tipped, with two nodulose spiral cords; teleoconch whorls heavily nodulose; anterior canal short to moderately long, usually subtubular (based on Wilson, 1993).

Isotriphora tigrina new species
(Figures 7–8, 39–44)

Triphora sp. 4: Leal (1991: 124, pl. 17, figs. C–D).
Triphora sp.: Absalão et al. (2006: 238, in part).

Type Material: Holotype: MNRJ 25992. Paratypes: REVIZEE C5-49R: MNRJ 16227 [2], IBUFRJ 17051 [2]; type locality: MZSP 105154 [3], MNRJ 25993 [7], MNHN IM-2012-2110 [8].

Type Locality: Trindade Island, Vitória-Trindade Chain, Brazil (20°30′ S, 29°19′ W, 52–60 m). Station 35-DC59 of the Expedition MD55.

Other Material Examined: IBUFRJ 14667, REVIZEE C5-49R [3]; IBUFRJ 14718, REVIZEE C5-48R [3]; MNRJ 25029, MD55 21-DC35 [2]; MNRJ 25030, MD55 35-DC59 [1]; MNHN, Enseada dos Portugueses, Trindade Is., v/1987 [1]; MZSP 100957, Cairu, Morro de São Paulo, Bahia, Petrônio Coelho-Filho coll., 2011 [1].

Diagnosis: Shell with a truncated apex; teleoconch with two main spiral cords, the abapical one with brown inter-nodular spaces during most of the shell; subperipheral cord and two basal cords brown and smooth.

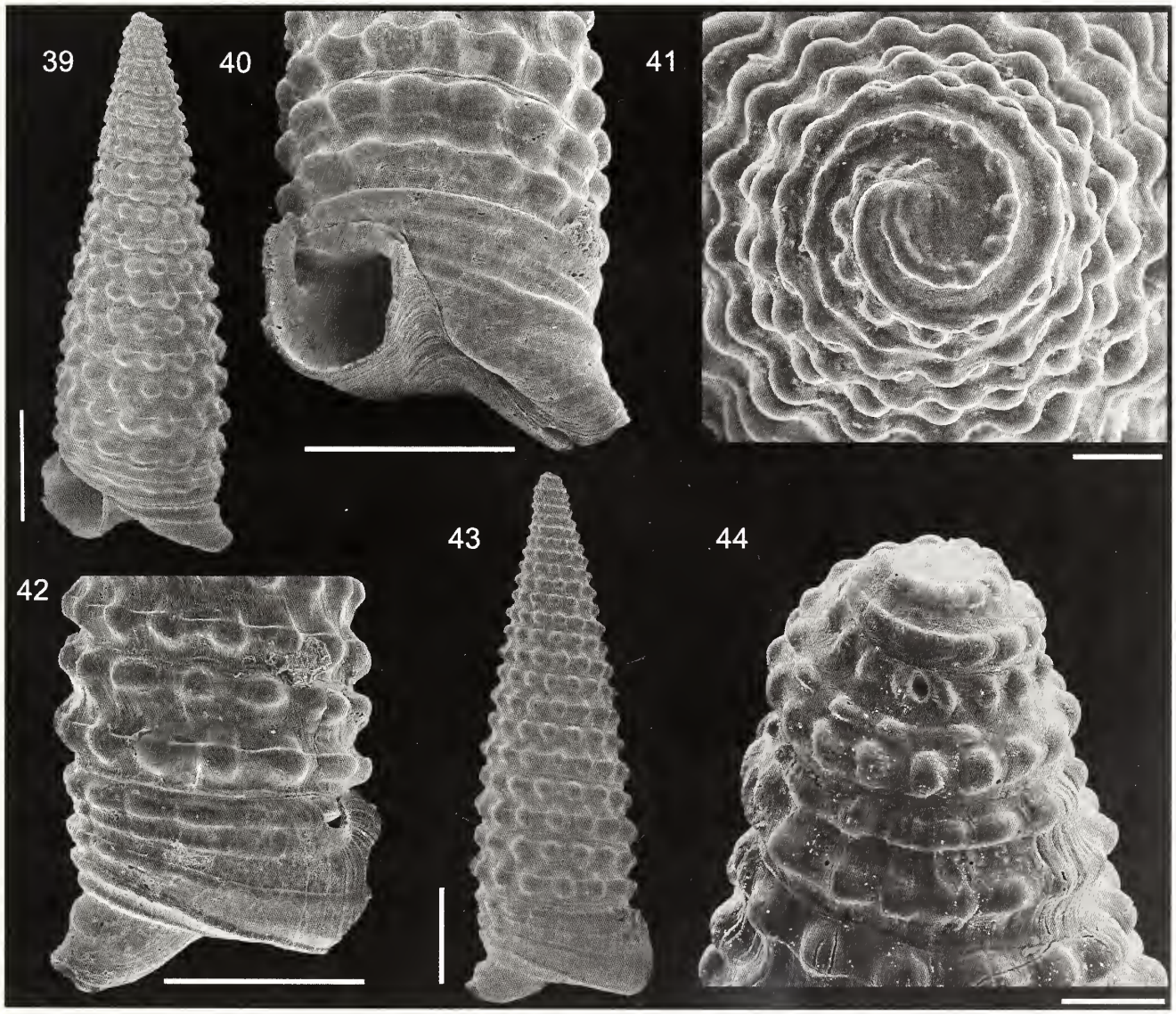
Description: Shell elongated, conical, reaching 5.2 mm in length, 1.4 mm in width, with up to 13 whorls. Paucispiral protoconch with truncated apex and without clear differentiation from teleoconch. After the very narrow nucleus, two white spiral cords (one adapical and one small median) and a brown abapical spiral cord emerge; after approximately one whorl the small median spiral cord disappears, almost simultaneously with a change in color of abapical spiral cord (brown to white) and adapical spiral cord (white to brown) on next whorl; adapical spiral cord tinted with brown for ~ two whorls, where it gradually fades, assuming color of shell background, which varies from creamy to light brown; simultaneously, abapical spiral cord becomes brown in inter-nodular spaces, until shell ends. Nodules of abapical spiral cord more spaced than adapical one; at the 11th whorl, a very small and wavy median spiral cord appears very close to adapical one; suture barely distinct, with a small cord more visible on last whorls; subperipheral cord and two basal cords, all smooth and brown; aperture ovoid, with a small posterior canal; outer lip well projected to front of shell; long and nearly closed siphonal canal, curving downward/backward. Animal unknown.

Etymology: This species is named for its brown subperipheral and basal cords, resembling the stripes of a tiger.

Remarks: A similar species to *I. tigrina* in the western Atlantic is *Isotriphora guanahacabibes* Rolán and Fernández-Garcés, 2008, a species from Caribbean. However *I. tigrina* has a unique color pattern of brown bands, in the adapical spiral cord of earlier whorls and

mainly in the inter-nodular spaces of the abapical spiral cord of the remaining whorls (instead of the whitish shells of *I. guanahacabibes*) (Figures 7–8); two distinct basal cords (while *I. guanahacabibes* has only one) (Figure 40), and a later development of the median spiral cord (in the 11th whorl of the shell in *I. tigrina*, ninth in *I. guanahacabibes*, as figured in Rolán and Fernández-Garcés, 2008). *Isotriphora peetersae* (Moolenbeek and Faber, 1989), another species from Caribbean, has a totally different color than *I. tigrina*, with about five initial whorls of the shell being white and the remainder dark brown, in addition to a median spiral cord appearing on the fourth/fifth whorl of the teleoconch. *Isotriphora taenialba* Rolán and Espinosa, 1994, a species from Cuba, has the adapical spiral cord of the teleoconch and suture dark brown, and the median spiral cord becomes nodulous much earlier on the fourth/fifth whorl of the teleoconch.

Isotriphora tigrina shares with *Iniforis carmelae* and *Iniforis pseudothomae* the discontinuous brown color on the abapical spiral cord of the teleoconch, but in *I. tigrina* this color is mainly restricted to the inter-nodular spaces. The protoconch typical of the genus *Isotriphora* (with nodular spiral cords) (Figure 44), the presence of a smooth subperipheral cord (Figure 40) and a small posterior canal above the aperture (not deflected to the other side of the shell, as in *Iniforis*) are other features that distinguish *I. tigrina* from these two species. Also, a small and non-tuberculated median spiral cord appears on the teleoconch of *I. tigrina* (Figures 39–40), while *I. pseudothomae* never develops it.



Figures 39–44. *Isotriphora tigrina* new species. **39, 43.** Entire shell. **40, 42.** Last whorl and base. **41.** Adapical view of protoconch. **44.** Protoconch and beginning of teleoconch. 39–40, 42–44. MNRJ 25993, paratype. 41. IBUFRJ 14718. Scale bar = 1 mm to figures 39–40, 42–43, 100 μm to figures 41, 44.

Distribution: Brazil: Bahia state and Vitória-Trindade Chain (this study).

***Isotriphora onca* new species**
(Figures 9–10, 45–50)

Triphora sp.: Absalão et al. (2006: 238, in part).

Type Material: Holotype: MNRJ 16236. Paratypes: MD55 27-DC47: MNHN IM-2012-2111 [1]; REVIZEE C5-42R: MZSP 112068 [2], IBUFRJ 14367 [7], MNRJ 16230 [8].

Type Locality: Trindade Island, Vitória-Trindade Chain, Brazil (20°30'S, 29°16'W, 360 m). Station C5-41F of REVIZEE-Central.

Other Material Examined: IBUFRJ 12123, REVIZEE C5-42R [1]; IBUFRJ 14411, REVIZEE C5-42R [22]; MNRJ 16232, REVIZEE C5-42R [4]; MNRJ 17918, REVIZEE C5-42R [3].

Diagnosis: Shell with a truncated apex; color creamy to light brown, except the whitish apex; teleoconch with two main spiral cords.

Description: Shell elongated, conical, reaching 5.6 mm in length, 1.4 mm in width, with up to 14 whorls. Paucispiral protoconch with truncated apex and without clear differentiation from teleoconch. After the very narrow nucleus two spiral cords emerge; after approximately one whorl the adapical spiral cord disappears, and a small cord starts to develop above that, becoming a new adapical spiral cord. Creamy to light brown background color, nodules slightly lighter, inter-nodular spaces slightly darker than background color, especially on abapical spiral cord; two–three initial whorls whitish, with a faded brown abapical spiral cord. Nodules of the abapical spiral cord may be slightly more spaced than adapical one; few shells have a very small median spiral cord after the 13th whorl, very close to adapical spiral cord; suture barely distinct, with a small cord more visible on last whorls; subperipheral cord and two basal cords, all smooth and of same color as background; adapical basal cord, closer to subperipheral cord, smaller and absent in a few shells; aperture ovoid, with small posterior canal; outer lip well projected to front of shell; long and nearly closed siphonal canal, curving downward/backward. Animal unknown.

Etymology: The specific name alludes to the jaguar (*Panthera onca*), due to the similarity with the previously described species, *Isotriphora tigrina*.

Remarks: This species resembles *I. tigrina*, including the general shape of the shell (although *I. onca* has a more slender profile), the truncated apex with similar development of the spiral cords, the suture barely distinct and the presence of two main spiral cords. However, *I. onca* has a different color pattern (Figure 9–10), being almost entirely creamy to light brown, with a whitish apex, and the subperipheral-basal cords are not tinted with brown. *Isotriphora onca* has a smaller (sometimes absent) adapical basal cord (Figure 46), in addition to narrower whorls and closer nodules on the abapical spiral cord of the teleoconch than *I. tigrina*. Also, the very small median spiral cord appears later on *I. onca*.

Isotriphora onca is distinguished from *I. guanahacabibes* by significant differences in color (whitish in *I. guanahacabibes*, or with small areas of light brown; creamy to light brown in *I. onca*, with the apex whitish) and the later development of the small median spiral cord on *I. onca*. As mentioned before, *I. peetersae* has about five whitish whorls on the beginning of the shell, instead of the two/three initial whorls on *I. onca*. Furthermore, the dark color on the remainder whorls on the teleoconch of *I. peetersae* (creamy to light brown in *I. onca*) and the earlier development of a strong median spiral cord clearly distinguishes both species. *Isotriphora taenialba* has a totally different color pattern and an earlier development of a strong median spiral cord.

Material from the type locality (including the holotype) was most likely deposited by turbidity currents, as all other shells were collected at shallower depths (~ 85-105 m).

Distribution: Brazil: Vitória-Trindade Chain (this study).

Genus *Latitriphora* Marshall, 1983

Type Species: *Triphora latilirata* Verco, 1909, original designation; Recent, southern Australia.

Diagnosis: Multispiral protoconch, embryonic shell with hemispherical granules, larval shell with two spiral threads and uninterrupted axial riblets; teleoconch with three spirals cords commencing simultaneously; nodules strongly flattened, with sharp edges that overhang sides of spirals (based on Marshall, 1983).

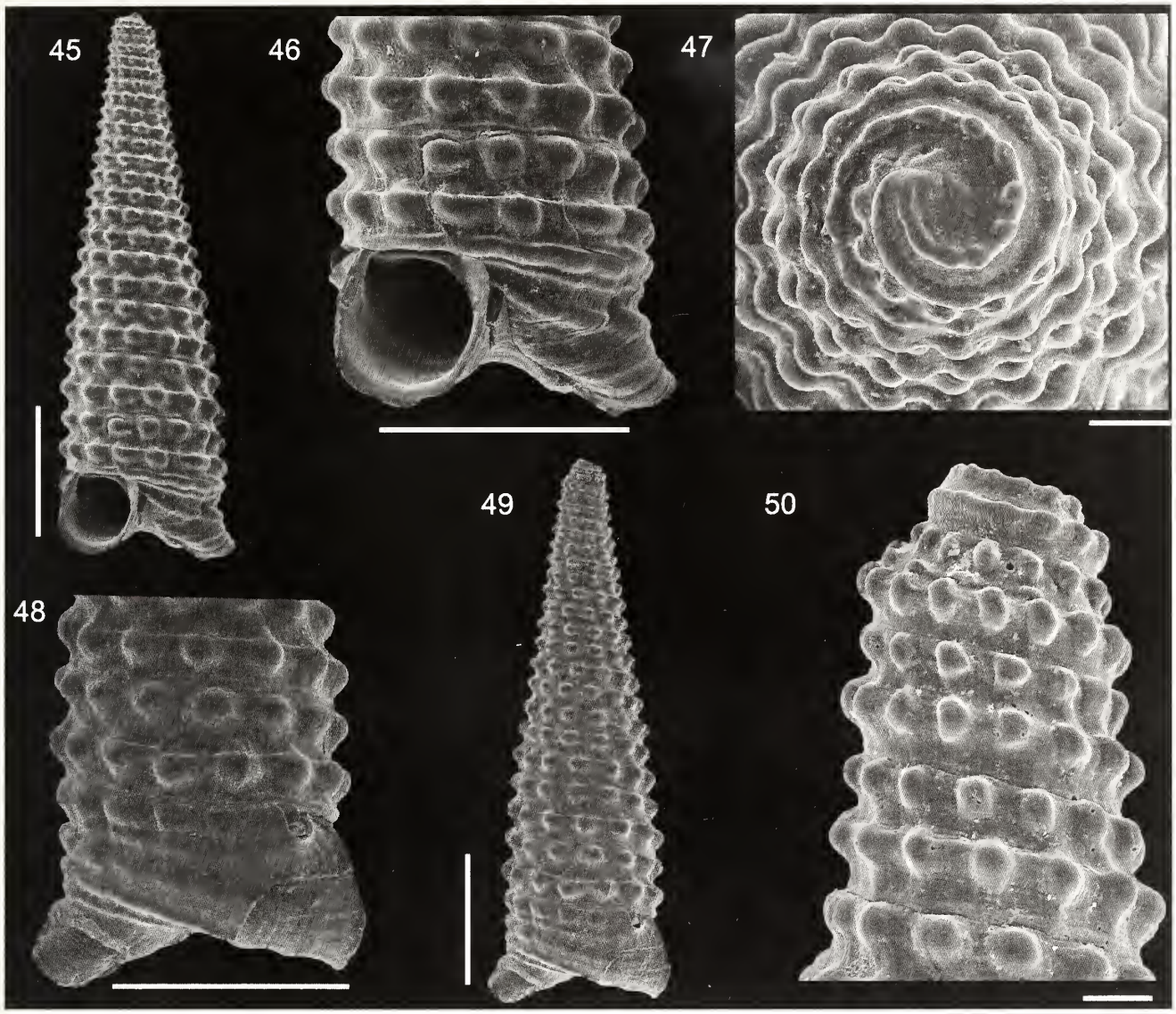
***Latitriphora albida* (A. Adams, 1854)**
(Figures 11, 22)

Triphoris albidus A. Adams (1854: 278).
Triforis (Sychar) samanae Dall (1889: 248); Dall and Simpson (1901: 423, pl. 54, fig. 18).
Triphora samanae: Jong and Coomans (1988: 51, pl. 34, fig. 245).
Triphora sp. 5: Leal (1991: 124).
Latitriphora albida: Rolán and Fernández-Garcés (1995: 14, figs. 29–32; 2007: 22, pl. III, figs. 8–9); Redfern (2001: 67, pl. 33, fig. 280); Lee (2009: 89, text-fig.).
Triphora decorata: Absalão et al. (2006: 238, in part) non C. B. Adams, 1850.

Type Material: Lectotype: NHM 196563. Paralectotype: NHM 196654.

Type Locality: Honduras.

Material Examined: MNRJ 17922, Praia do Andrada, Trindade Is., J. H. Leal, C. B. Castro and W. Zwink coll., 17/xii/1982 [1]; MNRJ 25005, Enseada dos



Figures 45–50. *Isotriphora onca* new species. **45, 49.** Entire shell. **46, 48.** Last whorl and base. **47.** Adapical view of protoconch. **50.** protoconch and beginning of teleoconch. **45–50.** MNRJ 16230, paratype. Scale bar = 1 mm to figures 45–46, 48–49, 100 µm to figures 47, 50.

Portugueses, Trindade Is., 10 m depth, P. Bouchet and J. H. Leal coll., 22/v/1987 [1]; MNRJ 25015, MD55 25-DC43 [1]; MNRJ 25016, MD55 9-DC22 [1].

Remarks: This is the only species of the genus *Latitriphora* at the West Atlantic. The shell of *L. albida* is very similar to that of *Nototriphora decorata*, but the teleoconch of *L. albida* has a more flattened profile of its axially elongated and very close-set beads (Figure 22). Also, the beads of the adapical spiral cord almost reach the beads of the abapical spiral cord of the adjacent whorl, and smaller and paler brown blotches are present on *L. albida* (Figure 11). The median spiral cord of the teleoconch of *L. albida* begins earlier—in the third whorl, following Lee (2009), instead of the transition between fourth and fifth whorl on *N. decorata* (Figure 25)—but it could not be determined in which whorl it develops in the material examined of *L. albida*, as all the shells had the apex broken. In the comments on *L. albida*, Lee (2009) cited that this species develops the median spiral cord later than *N. decorata*, when the opposite actually occurs.

Distribution: Bermuda (Jensen and Pearce, 2009); USA: Georgia (Rosenberg, 2009), Florida (Lee, 2009); Gulf of Mexico (Rosenberg et al., 2009); Bahamas (Redfern, 2001); Cuba (Rolán and Fernández-Garcés, 1995); Belize (Miloslavich et al., 2010); Honduras (type locality); Hispaniola (Miloslavich et al., 2010); Puerto Rico (Dall and Simpson, 1901, cited as *Triforis samanae*);

Colombia (Lee, 2009); ABC Islands (Jong and Coomans, 1988, cited as *Triphora samanae*); Brazil: Vitória-Trindade Chain (this study).

Genus *Coriophora* Laseron, 1958

Type Species: *Coriophora negrita* Laseron, 1958, original designation; Recent, western Pacific.

Diagnosis: Paucispiral or multispiral protoconch; on the latter, embryonic shell with hemispherical granules, larval shell with axial riblets crossed by a central spiral thread; teleoconch with a later development of median spiral cord; radular formula 24-1-1-1-24, central and marginal teeth with three cusps, lateral teeth with four to five cusps (based on the diagnosis of *Mesophora* on Marshall, 1983 and Wilson, 1993).

Synonym: *Mesophora* Laseron, 1958 non Borgmeier, 1937; see Özdikmen (2013).

***Coriophora novem* (Nowell-Usticke, 1969)**
(Figures 12, 23, 33)

Triphora novem Nowell-Usticke (1969: 12, pl. 2, fig. 20); Jong and Coomans (1988: 49, pl. 34, fig. 236).
Triphora sp. indet. A: Odé (1989: 111, fig. 6).
Marshallora sp. 1: Leal (1991: 121, pl. 16, figs. H–I).
Mesophora aff. *novem*: Rolán and Fernández-Garcés (1995: 11, figs. 12–16).
Mesophora novem: Rolán and Fernández-Garcés (1995: 11, figs. 8–11; 2007: 23, pl. IV, figs. 1–5); Redfern (2001: 67, pl. 33, fig. 282); Lee (2009: 90, text-fig.); Tunnell et al. (2010: 205, text-fig.); Garcia and Lee (2011).
Triphora decorata: Absalão et al. (2006: 238, in part) non C. B. Adams, 1850.
Triphora melanura: Absalão et al. (2006: 238, in part) non C. B. Adams, 1850.
Triphora nigrocincta: Absalão et al. (2006: 238); Gomes et al. (2006: 187) non C. B. Adams, 1839.
Triphora sp.: Absalão et al. (2006: 238, in part).

Type Material: Holotype: AMNH 195419.

Type Locality: Virgin Islands.

Material Examined: IBUFRJ 11992, REVIZEE C5-42R [1]; IBUFRJ 19442, REVIZEE C5-30R [1]; IBUFRJ 19444, REVIZEE C1-C61 [4]; IBUFRJ 19452, REVIZEE C5-49R [1]; IBUFRJ 19453, REVIZEE C1-C61 [1]; MNRJ 25006, MD55 16-DC29 [1]; MNRJ 25007, MD55 9-DC22 [1]; MNRJ 25008, MD55 35-DC59 [1]; MNRJ 25009, MD55 25-DC43 [2]; MNRJ 25010, MD55 23-DC41 [1]; MNRJ 25011, MD55 21-DC35 [1]; MZSP 105164, Enseada dos Portugueses, Trindade Is., v/1987 [1]; MNHN, MD55 35-DC59 [1]; MNHN, MD55 20-DC34 [1].

Other Material Examined: Sulphur Bank: IBUFRJ 13321, REVIZEE C5-13R, 16°47′ S, 37°41′ W, 50 m, 30/vi/2001 [1].

Remarks: This is the only species of the genus *Coriophora* at the West Atlantic. The shells here identified as *C. novem* exhibit a unique color pattern, with the three initial whorls of the teleoconch white and the others with a brown background and violet/greyish nodules (Figure 12). The median spiral cord appears around the eighth/ninth whorl of the teleoconch, or even at the end of the seventh whorl, but always closer to adapical spiral cord (Figure 23).

Rolán and Fernández-Garcés (1995) distinguished two morphs, *M. novem* and *M.* aff. *novem*; later the two morphs were named as *M. novem* only (Rolán and Fernández-Garcés, 2007). The shells herein examined are much more similar to *M.* aff. *novem* sensu Rolán and Fernández-Garcés (1995), especially with respect to the darker teleoconch color (except for the initial white whorls), the same color between the spiral cords (and also lacking a darker adapical spiral cord) and the apparent shorter length of the siphonal canal when compared to the figures 3 and 4 (plate IV) of Rolán and Fernández-Garcés (2007). The few shells with protoconch in the material here examined initially present two spiral cords in the larval shell with the subsequent disappearance of the adapical one later on the first whorl of larval shell, strengthening of this cord at the end of the second whorl, and later disappearance of this cord on the last whorl (Figure 33), again similar to *M.* aff. *novem* of Rolán and Fernández-Garcés (1995). The shells of *C. novem* from Cuba have two spiral cords throughout the larval shell (Rolán and Fernández-Garcés, 1995). Conservatively, we prefer to regard this darker morph also as *C. novem*.

The shells illustrated by Tunnell et al. (2010) and Garcia and Lee (2011) as *M. novem* appear to be its darker morph, just like the brief description of this species in Lee (2009). In contrast, Redfern (2001) describes the paler morph.

Although Marshall (1983) and Wilson (1983) reported that the protoconch of *Mesophora* (synonym of *Coriophora*) bears only one spiral cord, Laseron (1958) considered that the protoconch in this genus "may be singly or doubly keeled," which supports the allocation of this species to *Mesophora* by Rolán and Fernández-Garcés (1995). The radular formula 24-1-1-1-24 of *Mesophora* (Marshall, 1983) is different from that of *M.* aff. *novem* (actually *C. novem*) in Rolán and Fernández-Garcés (1995), 12-1-1-1-12, although the number of cusps in each tooth cohort is the same.

Marshallora gutta Fernandes and Rolán, 1988, a species from Cape Verde, has some similarities with the shells herein studied. It includes protoconch features (high density of granules on the first whorl; presence of two spiral cords, except the initial whorls and the very end of the protoconch), the initial whorls of the teleoconch being white, large size of the rounded nodules, suture indistinct and later development of the median spiral cord. The main differences between the two species include some anatomical (like the radular formula) and shell features (*C. novem* has more nodulose subperipheral and basal cords, a homogeneous color on

base and a major extension of the white color on the beginning of the teleoconch).

The material that Absalão et al. (2006) named as *Triphora nigrocincta* (C. B. Adams, 1839) to REVIZEE-Central (IBUFRJ 11992 to the Vitória-Trindade Chain; IBUFRJ 13321, to the Sulphur Bank, near Abrolhos), and Gomes et al. (2006) reproduced, is actually formed by two shells of *C. novem*.

The single shell of *C. novem* collected at the station MD55 16-DC29 (depth of 310–350 m) is probably a taphonomic anomaly (possibly resulting from deposition by turbidity currents), as the remaining shells from Vitória-Trindade Chain and records in the literature indicate that this species is observed only in shallower depths (~ 20–105 m).

Distribution: USA: Florida (Lee, 2009), Louisiana (Garcia and Lee, 2002), Texas (Tunnell et al., 2010); Gulf of Mexico (Rosenberg et al., 2009); Bahamas (Redfern, 2001); Cuba (Rolán and Fernández-Garcés, 1995); Jamaica (Rosenberg, 2009); Puerto Rico (Lee, 2009); Virgin Islands (type locality); ABC Islands (Jong and Coomans, 1988); Brazil: Sulphur Bank and Vitória-Trindade Chain (this study).

Genus *Monophorus* Grillo, 1877

Type Species: *Trochus perversus* Linnaeus, 1758, by monotypy; Recent, Europe and northern Africa.

Diagnosis: Paucispiral or multispiral protoconch; on the latter, embryonic shell with cruciform tubercles, larval shell with axial riblets crossed by two median spiral cords, with or without a smooth spiral zone; teleoconch with a later development of median spiral cord; radular formula (8-12)-1-1-1-(8-12), central tooth with five cusps, lateral teeth with five to seven cusps, most of marginal teeth with four to five cusps (based on Marshall, 1983).

Synonyms: *Biforina* Bucquoy, Dautzenberg and Dollfus, 1884; *Notosinister* Finlay, 1927; according to Marshall (1983).

Monophorus olivaceus (Dall, 1889)
(Figures 13, 24, 34)

Triforis decorata var. olivacea Dall (1889: 244).

Triphora ornata auct. non Deshayes, 1832: Warmke and Abbott (1962: 76, pl. 13, fig. i); Rios (1970: 45, not illustrated; 1975: 51, pl. 13, fig. 189; 1985: 161, pl. 53, fig. 763; 1994: 95, pl. 31, fig. 376; 2009: 173, text-fig.); Jong and Coomans (1988: 50, not illustrated); Absalão (1989: 3, not illustrated); Merlano and Hegedus (1994: 149, pl. XLVI, fig. 527); Absalão and Pimenta (2005: 29, fig. 64); Absalão et al. (2006: 238, in part); Gomes et al. (2006: 187;not illustrated); Santos et al. (2007: 226; not illustrated).

Triphora (Cosmotriphora) ornata auct. non Deshayes, 1832: Odé (1989: 110).

Triphora sp. 1: Leal (1991: 122).

Monophorus olivaceus: Rolán and Fernández-Garcés (1994: 17, figs. 1–3, 6, 8, 30 MO; 2007: 23, pl. IV, figs. 23–27; 2008: 87, figs. 4 B–F, H–K); Redfern (2001: 67, pl. 33, fig. 284); Espinosa and Ortea (2001: 20, not illustrated); Lee (2009: 90, text-fig.); Garcia and Lee (2011).

Triphora sp.: Absalão et al. (2006: 238, in part).

Cosmotriphora ornata auct. non Deshayes, 1832: Tunnell et al. (2010: 204, text-fig.).

Type Material: Lectotype: MCZ 7379.

Type Locality: Key West, west of Florida, Gulf of Mexico, 91 m.

Material Examined: MNRJ 25025, MD55 23-DC41 [1]; MNRJ 25026, MD55 20-DC34 [2]; MNRJ 25027, MD55 13-DC26 [2]; MNRJ 25028, MD55 10-DC24 [1]; MNHN, MD55 20-DC34 [2].

Remarks: In this species, the adapical and median (appearing later) spiral cords of the teleoconch have the color pattern of one white bead usually intercalary between two or three brown beads, although not being a rule, and the abapical spiral cord is white (Figure 13). *Monophorus olivaceus* has a large shell size for the family, up to 14.77 mm and 14 whorls of teleoconch in the shells of this study (apex missing).

Monophorus aterallbus Rolán and Fernández-Garcés, 1994 is the other species of *Monophorus* from the West Atlantic. The shell of *M. aterallbus* has continuous dark brown color on adapical and median spiral cords, while *M. olivaceus* has a discontinuous brown and white color on these cords.

According to Faber and Moolenbeek (1991) and Rolán and Fernández-Garcés (2008), the previous records of *Triphora ornata* from the western Atlantic (e.g. Abbott, 1974; Jong and Coomans, 1988; Rios, 1994) actually represent *M. olivaceus*, since the type material of *T. ornata* does not match the western Atlantic species (Rolán and Fernández-Garcés, 2008).

Triphora sp. 1 in Leal (1991) is herein considered to be *M. olivaceus*. However, the record of *Triphora ornata* by Leal (1991), based on material from Fernando de Noronha Archipelago (off Brazil), is pending examination, since it was not illustrated.

Monophorus olivaceus is reported to show some variation in size and in hue of its brown color, as pointed in the original description and in Rolán and Fernández-Garcés (2007; 2008). Also, Rolán and Fernández-Garcés (2008) included a shell from Florida with a predominant white coloration on the median spiral cord of the teleoconch as belonging to this species.

Distribution: USA: Florida (type locality), Louisiana (Lee, 2009), Texas (Tunnell et al., 2010, cited as *Cosmotriphora ornata*); Gulf of Mexico (Rosenberg et al., 2009); Bahamas (Redfern, 2001); Cuba (Rolán and Fernández-Garcés, 1994); Belize (Miloslavich et al., 2010); Virgin Islands; St. Vincent; Grenada (Rolán and Fernández-Garcés, 2008); Costa Rica (Espinosa and Ortea,

2001); Colombia (Merlano and Hegedus, 1994, cited as *Triphora ornata*); Venezuela (Rolán and Fernández-Garcés, 2008); ABC Islands (Jong and Coomans, 1988, cited as *T. ornata*); Brazil: Amapá to Bahia (Rios, 1985, cited as *T. ornata*), Fernando de Noronha and Abrolhos (Rios, 1985; Gomes et al., 2006, cited as *T. ornata*), Vitória-Trindade Chain (this study), Espírito Santo (Absalão, 1989, cited as *T. ornata*), Rio de Janeiro (Absalão, 1989; Absalão and Pimenta, 2005; Santos et al., 2007; cited as *T. ornata*).

Genus *Nototriphora* Marshall, 1983

Type Species: *Notosinister aupouria* Powell, 1937, original designation. Recent, New Zealand.

Diagnosis: Paucispiral or multispiral protoconch; on the latter, embryonic shell with hemispherical granules, larval shell with axial riblets crossed by two median spiral cords, the adapical one initially strong, but soon weakening and reappearing later; teleoconch with a later development of median spiral cord; radular formula 9-1-1-1-9, central tooth with three cusps, lateral teeth with four cusps, marginal teeth with short outer cusps and long median cusps (based on Marshall, 1983).

Nototriphora decorata (C. B. Adams, 1850)
(Figures 14, 25, 35)

Cerithium decoratum C. B. Adams (1850: 117); Clench and Turner (1950: 272, pl. 38, fig. 2).
Triphoris variegatus A. Adams (1854: 277).
Triforis arthuri Jousseaume (1884: 221) [*nomen nudum*].
Triphora decorata: Rios (1970: 45, not illustrated; 1975: 50, pl. 13, fig. 186; 1985: 160, pl. 53, fig. 760; 1994: 94, pl. 31, fig. 373; 2009: 172, text-fig.); Abbott (1974: 111, fig. 1133); Jong and Coomans (1988: 51, not illustrated); Absalão (1989: 3, not illustrated); Leal (1991: 122, pl. 16, figs. J–K); Merlano and Hegedus (1994: 148, pl. XLVI, fig. 521); Absalão et al. (2006: 238, in part); Gomes et al. (2006: 187; not illustrated); Santos et al. (2007: 226, not illustrated).
Triphora (Cosmotriphora) decorata: Odé (1989: 110, fig. 5).
Nototriphora decorata: Rolán and Fernández-Garcés (1994: 19, figs. 10, 14, 16, 30 ND; 2007: 24, pl. V, figs. 1–5); Redfern (2001: 68, pl. 33, fig. 285); Espinosa and Ortea (2001: 20, not illustrated); Lee (2009: 91, text-fig.); Tunnell et al. (2010: 206, text-fig.).
Triphora sp.: Absalão et al. (2006: 238, in part).

Type Material: Lectotype: MCZ 186178.

Type Locality: Jamaica.

Material Examined: IBUFRJ 9313, REVIZEE C1-C61 [2]; IBUFRJ 19445, REVIZEE C5-44R [1]; IBUFRJ 19450, REVIZEE C5-48R [1]; IBUFRJ 19454, REVIZEE C1-C62 [4]; IBUFRJ 19456, REVIZEE C1-C62 [6]; MNRJ 17924, REVIZEE C5-42R [1]; MNRJ 25001, MD55 35-DC59 [3]; MNRJ 25002, MD55 9-DC22 [1]; MNRJ 25003, MD55 13-DC26 [1]; MNHN, MD55 20-DC34 [3]; MNHN, Enseada dos Portugueses, Trindade Is., v/1987 [5].

Remarks: This is a very common species in Brazil and the only representative of the genus *Nototriphora* on the West Atlantic. Its teleoconch has brown spots over a creamy-white background (Figure 14), and the median spiral cord appears around the fourth/fifth whorl (Figure 25). This pattern of coloration on *N. decorata* can cause problems in separating this species from other triphorids. In addition to significant differences on the protoconch (e.g., number of spiral cords on larval shell), the shell of *Nototriphora decorata* has a more axial and irregular pattern of brown spots than *Monophorus olivaceus*, which has a more spiral pattern (and its abapical spiral cord never shows beads tinted with brown, contrary to *N. decorata*). Also, the median spiral cord appears later in the teleoconch of *M. olivaceus*, only around the fifth/sixth whorl (Rolán and Fernández-Garcés, 1994) or after the seventh whorl (Lee, 2009). *Nototriphora decorata* has more numerous and smaller nodules than *M. olivaceus*, contrary to Abbott (1974), as pointed out by Odé (1989) and Lee (2009). The differences between *N. decorata* and *Latitriphora albida* / *Cosmotriphora arnoldoi* were mentioned in the remarks under the last two species.

Lee (2009) recognized intraspecific variation in *N. decorata*, with a morph delicately beaded and with blotches present at any of the three spiral cords, and another coarsely beaded and with dark blotches restricted to the adapical and median spiral cords. The shells here examined correspond to Lee's (2009) first morph (Figure 14). Beyond that, Rolán and Fernández-Garcés (2008) commented on a violet coloration (instead of brown) in some shells of *N. decorata* from Cuba, possibly resultant of an ecological variation.

Nototriphora decorata is reported to have an amphi-Atlantic distribution in some works (e.g. Leal, 1991; Rios, 1994, 2009), but it is actually due to a confusion with the eastern Atlantic distribution of *Nototriphora canarica* (Nordsieck and Talavera, 1979), initially described as a subspecies of *N. decorata* and later elevated to species by Bouchet (1985).

According to Rolán and Fernández-Garcés (2008), *Triphoris variegatus* A. Adams, 1854 is a synonym of *N. decorata*. *Triforis arthuri* Jousseaume, 1884, *nomen nudum*, was proposed as a replacement name for *Triphoris variegatus* A. Adams, 1854 non *Cerithium variegatum* C. B. Adams. However, *Cerithium variegatum* C. B. Adams does not exist, being created as result of a *lapsus calami* by Jousseaume (1884) while copying the list of names of both C. B. Adams and A. Adams presented by Mörch (1875).

Distribution: Bermuda (Jensen and Pearce, 2009); USA: North Carolina (Rosenberg, 2009), Florida (Lee, 2009), Louisiana (Garcia and Lee, 2002), Texas (Tunnell et al., 2010); Gulf of Mexico (Rosenberg et al., 2009);

Bahamas (Redfern, 2001); Cuba (Rolán and Fernández-Garcés, 1994); Jamaica (type locality); Belize; Puerto Rico; Lesser Antilles (Miloslavich et al., 2010); Costa Rica (Espinosa and Ortea, 2001); Panama; Colombia; Venezuela (Miloslavich et al., 2010); ABC Islands (Jong and Coomans, 1988); Brazil: Amapá to Rio de Janeiro (Rios, 1985), Fernando de Noronha and Vitória-Trindade Chain (Leal, 1991; Gomes et al., 2006).

Genus "*Triphora*" Blainville, 1828

Type Species: *Triphora gemmatum* Blainville, 1828, by monotypy. Recent, Mauritius.

Remarks: Although Marshall (1983) tried to define a diagnosis for *Triphora*, this genus still has uncertain limits. It is commonly used as a "catch-all" taxon when generic assignment is not possible, as "*Triphora*" s.l. (Rolán and Fernández-Garcés, 2008; Lee, 2009).

Synonyms: *Tristoma* Menke, 1830; *Triphoris* Deshayes, 1832 (orthographic variant), non *Triforis* Deshayes, 1834; according to Marshall (1983).

***Triphora atlantica* (Smith, 1890)**
(Figures 15, 26, 36)

Triforis atlantica Smith (1890: 292, pl. XXI, fig. 26).
Triphora decorata: Absalão et al. (2006: 238, in part) non C. B. Adams, 1850.
Triphora melanura: Absalão et al. (2006: 238, in part) non C. B. Adams, 1850.
Triphora pulchella: Absalão et al. (2006: 238, in part) non C. B. Adams, 1850.
Triphora turristhomae: Absalão et al. (2006: 238, in part) non Holten, 1802.
Triphora sp.: Absalão et al. (2006: 238, in part).
Triphora atlantica: Rolán and Fernández-Garcés (2008: 146, figs. 25 A–I); Lee (2009: 92, text-fig.); Garcia and Lee (2011).

Type Material: Lectotype and paralectotypes on NHM 89.10.1.1874-93.

Type Locality: St. Helena Island.

Material Examined: IBUFRJ 13142, REVIZEE C2-22R [2]; IBUFRJ 14422, REVIZEE C5-30R [3]; IBUFRJ 19446, REVIZEE C1-C62 [1]; MNRJ 25012, MD55 35-DC59 [1]; MZSP 105148, Enseada dos Portugueses, Trindade Is., v/1987 [1].

Remarks: The shells examined agree with the lectotype designated by Rolán and Fernández-Garcés (2008), as with the description given by the authors. The teleoconch of *T. atlantica* has a brown abapical spiral cord with lighter nodules, while the adapical spiral cord is white with slightly darker inter-nodular spaces (Figure 15). A median spiral cord appears on the eight/ninth whorl of the teleoconch (Figure 26). The larval shell begins with one spiral cord, later developing an additional spiral cord (the adapical one), which fades in the last whorl (Figure 36). Compared to a shell from Florida (figure 25-I on Rolán and Fernández-Garcés, 2008), the development of the adapical spiral cord of protoconch seems to occur later on the shells of *T. atlantica* from the Vitória-Trindade Chain (Figure 36). Rolán and Fernández-Garcés (2008) described the axial ribs as being prosocline, but they are actually opisthocline.

Triphora atlantica has a wide distribution throughout the Atlantic Ocean, and its type locality is an island in the south-central Atlantic; however, few Caribbean records are given for this species. The shells figured in Abbott (1974) as *Triphora lilacina* (Dall, 1889) may be *T. atlantica*, as pointed out by Rolán and Fernández-Garcés (2008) and Lee (2009). The shell drawn in the original description (Smith, 1890) does not show the brown color on the abapical spiral cord of the body whorl, possibly due to an oversight by the author.

Distribution: USA: Florida (Lee, 2009), Louisiana (Lee, 2009); Puerto Rico (Rolán and Fernández-Garcés, 2008); St. Helena (type locality); Brazil: Espírito Santo (Rolán and Fernández-Garcés, 2008), Vitória-Trindade Chain (this study).

***Triphora ellyae* Jong and Coomans, 1988**
(Figures 16, 27, 37)

Triphora ellyae Jong and Coomans (1988: 50, pl. 34, fig. 242); Rolán and Fernández-Garcés (1995: 13, figs. 23-25; 2007: pl. V, figs. 17–21); Lee (2009: 92, text-fig.).
Triphora orteai Espinosa (2001: 21, fig. 7).
Triphora sp.: Absalão et al. (2006: 238, in part).

Type Material: Holotype: ZMA 3.87.072.

Type Locality: Aruba/Curaçao (ABC Islands).

Material Examined: IBUFRJ 14637, REVIZEE C5-48R [2]; Bacia de Campos, Rio de Janeiro state: MNRJ 15400, 22°42′ S, 40°40′ W, 5 m, iii/2007 [9]; MNRJ 18753, 22°42′ S, 40°40′ W, 110–120 m, 2006 [5]; MNRJ 18955, 22°42′ S, 40°40′ W, 5–10 m [2].

Remarks: As the two shells from Vitória-Trindade Chain were eroded, although allowing a taxonomic determination, we illustrated a shell from Bacia de Campos (Campos Basin), deposited at the molluscan collection of MNRJ (Figures 16, 27, 37). The shells examined have an ovoid shape, with almost all the shell being brown, except the white adapical spiral cord of the teleoconch and the entire first whorl of teleoconch (Figure 16). Also, the nodules of the median and abapical spiral cords are lighter than the background color. The median spiral cord develops in the fifth/sixth whorl of the teleoconch, and the base is short, with three smooth cords (including the subperipheral cord) (Figure 27). The shells here studied showed some color variation on the base, which can be light brown to whitish, with the subperipheral and basal cords slightly darker.

Triphora ellyae can be best differentiated from *T. atlantica* by the earlier development of the median spiral cord (fifth/sixth whorl of teleoconch in *T. ellyae*, eight/ninth whorl in *T. atlantica*), the darker brown median spiral cord, and the smooth subperipheral cord (very nodulose in *T. atlantica*). Further, the shell of *T. ellyae* is smaller than *T. atlantica* and it has a slight ovoid shape.

The study of the animal described by Espinosa (2001) as *Triphora orteai* (synonymized by Rolán and Fernández-Garcés, 2008 with *T. ellyae*) may point to the generic position of this species.

Distribution: USA: Florida, Louisiana (Lee, 2009); Gulf of Mexico (Rosenberg et al., 2009); Cuba (Rolán and Fernández-Garcés, 1995); Costa Rica (Espinosa, 2001, cited as *Triphora orteai*); ABC Islands (type locality); Brazil: Vitória-Trindade Chain and Rio de Janeiro state (this study).

***Triphora elvirae* Jong and Coomans, 1988**
(Figures 17, 28, 38)

Triphora elvirae Jong and Coomans (1988: 50, pl. 34, fig. 240); Rolán and Fernández-Garcés (1995: 13, figs. 20–22; 2007: pl. V, figs. 22–23); Garcia and Lee (2011).
Cosmotriphora elvirae: Redfern (2001: 65, pl. 32, fig. 273).
Triphora pulchella: Absalão et al. (2006: 238, in part) non C. B. Adams, 1850.
Triphora sp.: Absalão et al. (2006: 238, in part) non C. B. Adams, 1850.

Type Material: Holotype: ZMA 3.87.071.

Type Locality: Curaçao.

Material Examined: IBUFRJ 12105, REVIZEE C5-30R [1]; MNRJ 12771, REVIZEE C5-30R [2]; MNRJ 25031, MD55 9-DC22 [1]; MNRJ 25032, MD55 35-DC 59 [1]; MORG 51901, REVIZEE C1-C62 [3]; MNHN, MD55 23-DC40 [1]; MNHN, MD55 20-DC34 [1].

Remarks: This species has a brown abapical spiral cord, in contrast with the adapical and median white spiral cords (Figure 17). In addition to the abapical spiral cord, the teleoconch of *T. elvirae* also shows the subperipheral cord and usually the final portion of the base tinted with brown. In the shells examined, the median spiral cord appears in the seventh whorl of the teleoconch, showing the same size as the abapical spiral cord (the adapical one is slightly bigger) two whorls later (Figure 28). The material here studied is more similar to the shells of Cuba (Rolán and Fernández-Garcés, 1995) than to the holotype, which presents the light brown color of the abapical spiral cord extending beyond the nodules (Rolán and Fernández-Garcés, 1995).

Triphora elvirae is similar to *T. atlantica*, especially in the brown coloration on the abapical spiral cord; however, the coloration is continuous in *T. elvirae* (Figure 17) and restricted to the inter-nodular spaces on *T. atlantica* (Figure 15). The shell of *T. ellyae* has an ovoid shape and a brown median spiral cord on the teleoconch (Figure 16), while the shell of *T. elvirae* is conical and the median spiral cord of the teleoconch is white (Figure 17).

Redfern (2001) placed this species in *Cosmotriphora*, but this generical allocation requires further investigation, as the animal and radula have not yet been seen (Rolán and Fernández-Garcés, 1995). In addition to the description of protoconch of this species by Rolán and Fernández-Garcés (1995), the last whorl presents a weakening of the adapical spiral cord (Figure 38). Actually, the sequence of spiral cords on the protoconch of *T. elvirae* is similar to that observed on *Coriophora novem* (Figure 33).

The shell illustrated in Merlano and Hegedus (1994) as *Triphora intermedia* (C. B. Adams, 1850) appears to belong to *T. elvirae*.

Distribution: USA: Louisiana (Garcia and Lee, 2002); Gulf of Mexico (Rosenberg et al., 2009); Bahamas (Redfern, 2001); Cuba (Rolán and Fernández-Garcés, 1995); Belize (Miloslavich et al., 2010); Curaçao (type locality); Brazil: Vitória-Trindade Chain (this study).

DISCUSSION

Of the 13 species found in this study, *Cosmotriphora melanura* and *Nototriphora decorata* were previously reported from the Vitória-Trindade Chain. *Cosmotriphora arnoldoi*, *Iniforis carmelae*, *Iniforis pseudothomae*, *Latitriphora albida*, *Coriophora novem*, *Triphora ellyae* and *Triphora elvirae* were previously restricted to the Caribbean and Gulf of Mexico, although *L. albida* is also present in Bermuda and the southeastern coast of USA. These species are reported for the first time from Brazil. The known ranges of *Monophorus olivaceus* and *Triphora atlantica* in Brazil are herein extended to the Vitória-Trindade Chain.

Absalão et al. (2006) and Gomes et al. (2006) listed the occurrence of *Marshallora nigrocincta* (C. B. Adams, 1839), under the name *Triphora nigrocincta* (C. B. Adams, 1839), to the Vitória-Trindade Chain. As mentioned before, their taxonomic identification was erroneous, actually corresponding to *Coriophora novem*. Thus, the presence of *M. nigrocincta* at the study site is here invalidated. Furthermore, the occurrence of this species in Brazil needs further investigation as it may represent a complex of species (Bouchet, 1985).

The previous record of *Iniforis turristhomae* at the Vitória-Trindade Chain (Absalão et al., 2006) is here invalidated, as the single shell studied is very eroded, and it could not be positively identified.

Until now, only three species of *Isotriphora* were recognized in the western Atlantic (Rosenberg, 2009) and 11 worldwide (Rosenberg, 2011). *Isotriphora tigrina* new species is currently restricted to the Vitória-Trindade Chain and Bahia state and *Isotriphora onca* new species to the Vitória-Trindade Chain. The records of the two

species above represent the entirety of occurrences of *Isotriphora* for Brazil. The non-planktotrophic mode of development suggested by the protoconch in this genus indicates a greater possibility for endemism.

With the present study, the number of species of Triphoridae in the Vitória-Trindade Chain is increased from six to 15 and in Brazil from 17 to 26. Many other species still need to be described or otherwise reported from Brazil. Further scrutiny of this and other relatively understudied elements are certain to greatly improve our knowledge of the western Atlantic malacofauna in coming years.

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LITERATURE CITED

Abbott, R.T. 1974. American Seashells, 2nd Ed. New York, Van Nostrand Reinhold, New York, 663 pp.

Absalão, R.S. 1989. Padrões distributivos e zoogeografia dos moluscos da plataforma continental brasileira. Parte III. Comissão Oceanográfica Espírito Santo I. Memórias do Instituto Oswaldo Cruz 84 (4): 1-6.

Absalão, R.S. and A.D. Pimenta. 2005. Moluscos marinhos da APA do Arquipélago de Santana, Macaé, RJ. Rio de Janeiro, Ciência Moderna, 84 pp.

Absalão, R.S., C.H.S. Caetano, and R.R. Fortes. 2006. Filo Mollusca. pp. 211–260. In: H.P. Lavrado and B. L. Ignacio (eds.) Biodiversidade Bentônica da Região Central da Zona Econômica Exclusiva Brasileira. Rio de Janeiro, Museu Nacional, Série Livros 18, 389 pp.

Adams, A. 1854. Descriptions of new species of *Eulima*, *Triphoris*, etc., from the collection of Hugh Cuming. Proceedings of the Zoological Society of London 19: 276–279.

Adams, C.B. 1850. Descriptions of supposed new species of marine shells which inhabit Jamaica. Contributions to Conchology 7: 109–123.

Ardovini, R. and T. Cossignani. 2004. West African seashells. L'Informatore Piceno, Ancona, 320 pp.

Bouchet, P. 1985. Les Triphoridae de Méditerranée et du proche Atlantique (Mollusca, Gastropoda). Società Italiana di Malacologia 21: 5–58.

Bouchet, P. and J. P. Rocroi. 2005. Classification and nomenclator of gastropod families. Malacologia 47: 1–397.

Clench, W.J. and R.D. Turner. 1950. The Western Atlantic marine mollusks described by C.B. Adams. Occasional Papers on Mollusks 1 (15): 233–403.

Cossmann, M. 1906. Essais de paléoconchologie comparée. Paris, The Author and Rudeval, vol. 7, 215 pp.

Dall, W.H. 1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U. S. Coast Survey steamer "Blake", Lieut.-Commander C. D. Sigsbee, U. S. N., and Commander J. R. Bartlett, U. S. N., Commanding. XXIX - Report on the Mollusca. Part II - Gastropoda and Scaphopoda. Bulletin of the Museum of Comparative Zoology 18: 1–492, 40 pls.

Dall, W.H. 1892. Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River. Part II. Streptodont and other gastropods, concluded. Transactions of the Wagner Free Institute of Science of Philadelphia 3: [i–vii], 201–473, 1 fold-out map, pls. 13–22.

Dall, W.H. and C.T. Simpson. 1901. The Mollusca of Porto Rico. Bulletin of the United States Fish Comission 1: 351–524, pls. 53–58.

Dautzenberg, P. and H. Fischer. 1906. Mollusques provenant des dragages effectués à l'Ouest de l'Afrique pendant les campagnes scientifiques de S. A. S. le Prince de Monaco. Résultats des campagnes scientifiques accomplies sur son yatch par Albert 1er Prince Souverain de Monaco 32: 1–125.

Espinosa, J. 2001. Descripción de una nueva especie de *Triphora* (s. l.) Blainville, 1828. pp. 21–22. In: J. Espinosa and J. Ortea. Moluscos del Mar Caribe de Costa Rica: desde Cahuita hasta Gandoca. Avicennia 4: 1–77.

Espinosa, J. and J. Ortea. Moluscos del Mar Caribe de Costa Rica: desde Cahuita hasta Gandoca. Avicennia 4: 1–77.

Faber, M. J. 2010. Marine gastropods from the ABC islands and other localities 35. A new species of *Metaxia* (Gastropoda: Triphoridae). Miscellanea Malacologica 4 (3): 30.

Faber, M. J. and R. G. Moolenbeek. 1991. Two new shallow water triphorids and a new name in *Metaxia* from Florida and the West Indies. Apex 6 (3–4): 81–85.

Fernandes, F. and E. Rolán. 1988. A família Triphoridae (Mollusca: Gastropoda) no arquipélago de Cabo Verde. Publicações Ocasionais da Sociedade Portuguesa de Malacologia 11: 17–32, pls. I–IV.

Fernandes, M.R. and A.D. Pimenta. 2011. Taxonomic review of *Metaxia* (Gastropoda: Triphoridae) from Brazil, with description of a new species. Zoologia 28 (6): 819–830.

Garcia, E.F. and H.G. Lee. 2002. Report on molluscan species found in the offshore waters of Louisiana, including many extensions of known range and un-named species. American Conchologist 30 (4): 10–13.

Garcia, E.F. and H.G. Lee. 2011. Report on molluscan species found in the offshore waters of Louisiana, including many extensions of known range and un-named species. [www.jaxshells.org/efg1030.htm] URL, accessed on 12 March 2012.

Gomes, R.G., P.M.S. Costa, J.C. Monteiro, A.C.S. Coelho, and N.C. Salgado. 2006. Moluscos das ilhas oceânicas brasileiras. pp. 180–198. In: R. J. V. Alves and J. W. A. Castro (eds). Ilhas oceânicas brasileiras: da pesquisa ao manejo. Brasília, Ministério do Meio Ambiente, 340 pp.

Jensen, R.H. and T.A. Pearce. 2009. Marine mollusks of Bermuda – Checklist and Bibliography. Wilmington, Delaware Museum of Natural History, X + 473 pp.

Jong, K.M. and H.E. Coomans. 1988. Marine gastropods from Curaçao, Aruba and Bonaire. E.J. Brill, Leiden, 261 pp.

Jousseaume, F. 1884. Monographie des Triforidae. Bulletins de la Société Malacologique de France 1: 217–270.

Laseron, C.F. 1958. The Family Triphoridae (Mollusca) from Northern Australia; also Triphoridae from Christmas Island (Indian Ocean). Australian Journal of Marine and Freshwater Research 9 (4): 569–657.

Lavrado, H.P. 2006. Caracterização do ambiente e da comunidade bentônica. pp. 19–64. In: H.P. Lavrado and B.L. Ignacio (eds). Biodiversidade bentônica da região central da Zona Econômica Exclusiva Brasileira. Rio de Janeiro, Museu Nacional, Série Livros 18, 389 pp.

Leal, J.H. 1991. Marine prosobranch gastropods from oceanic islands off Brazil: Species composition and biogeography. Universal Book Services, Oegstgeest, X + 418 pp.

Lee, H.G. 2009. Marine shells of Northeast Florida. Jacksonville, Shell Club, 204 pp., 19 pls.

Özdikmen, H. 2013. Substitute names for three preoccupied generic names in Gastropoda. Munis Entomology and Zoology 8 (1): 252-256.

Marshall, B.A. 1977. The dextral triforid genus *Metaxia* (Mollusca: Gastropoda) in the south-west Pacific. New Zealand Journal of Zoology 4: 111–117.

Marshall, B.A. 1983. A revision of the recent Triphoridae of Southern Australia (Mollusca: Gastropoda). Records of the Australian Museum 2: 1–119.

Merlano, J.M.D. and M.P. Hegedus. 1994. Moluscos del Caribe Colombiano. Santa Fé de Bogotá, Colciencias, Fundación Natura, Invemar, 291 pp.

Miloslavich, P., J.M. Díaz, E. Klein, J.J. Alvarado, C. Díaz, J. Gobin, E. Escobar-Briones, J.J. Cruz-Motta, E. Weil, J. Cortés, A.C. Bastidas, R. Robertson, F. Zapata, A. Martín, J. Castillo, A. Kazandjian, and M. Ortiz. 2010. Marine biodiversity in the Caribbean: regional estimates and distribution patterns. PLoS ONE 5(8): e11916.doi: 10.1371/journal.pone.0011916.

Mörch, O.A.L. 1876. Synopsis molluscorum marinorum Indiarum occidentalium. Malakozoologische Blatter 23: 87–143.

Nowell-Usticke, G.W. 1969. A supplementary listing of new shells (illustrated). To be added to the check list of the marine shells of St. Croix. Published privately, 32 pp., 6 pls.

Nützel, A. 1998. Ueber die Stammesgeschichte der Ptenoglossa (Gastropoda). Berliner Geowissenschaftliche Abhandlungen, ser. E (Palaeobiologie) 26: 1–229.

Odé, H. 1989. Distribution and records of the marine Mollusca in the northwest Gulf of Mexico (a continuing monograph). Texas Conchologist 25:104–120.

O'Hara, T.D., M. Consalvey, H.P. Lavrado, and K.I. Stocks. 2010. Environmental predictors and turnover of biota along a seamount chain. Marine Ecology 31 (1): 84–94.

Redfern, C. 2001. Bahamian seashells – A thousand species from Abaco, Bahamas. Boca Raton, Bahamianseashells Inc., IX + 261 pp.

Rios, E.C. 1970. Coastal Brazilian seashells. Museu Oceanográfico do Rio Grande, Rio Grande, 255 pp.

Rios, E. 1975. Brazilian marine mollusks iconography. Museu Oceanográfico da FURG, Rio Grande, 331 pp.

Rios, E. 1985. Seashells of Brazil. Museu Oceanográfico da FURG, Rio Grande, 328 pp.

Rios, E. 1994. Seashells of Brazil. 2nd ed. Museu Oceanográfico da FURG, Rio Grande, 2nd ed., 368 pp.

Rios, E. 2009. Compendium of Brazilian seashells. Evangraf, Rio Grande, VIII + 668 pp.

Rolán, E. 2005. Malacological fauna from the Cape Verde Archipelago. Hackenheim, ConchBooks, 455 pp.

Rolán, E. and R. Fernández-Garcés. 1993. The family Triphoridae (Mollusca, Gastropoda) in Cuba. 2. The genus *Iniforis* Jousseaume, 1884. Apex 8 (3): 95–105.

Rolán, E. and R. Fernández-Garcés. 1994. The family Triphoridae (Mollusca, Gastropoda) in Cuba. 4. The genera *Monophorus, Nototriphora, Cosmotriphora and Cheirodonta*, with the description of three new species. Apex 9 (1): 17–27.

Rolán, E. and R. Fernández-Garcés. 1995. The family Triphoridae (Mollusca, Gastropoda) in Cuba. 5. The genera *Marshallora, Mesophora, Similiphora, Eutriphora, Latitriphora, Aclophora* and other species without generic affiliation. Apex 10 (1): 9–24.

Rolán, E. and R. Fernández-Garcés. 2007. Caribbean Triphoridae (Gastropoda: Triphoroidea): list and colour ilustrations. Neptunea 6 (3): 13–24.

Rolán, E. and R. Fernández-Garcés. 2008. New data on the Caribbean Triphoridae (Caenogastropoda, Triphoroidea) with the description of 26 new species. Iberus 26 (1): 81–170.

Rolán, E. and R. Fernández-Garcés. 2009. Two new species of *Iniforis* (Gastropoda: Triphoridae) from the Caribbean. Novapex 10 (3): 103–108.

Rosenberg, G. 2009. Malacolog 4.1.1: A Database of Western Atlantic Marine Mollusca, version 4.1.1 Available online at: http://www.malacolog.org.

Rosenberg, G. 2011. *Isotriphora* Cotton and Godfrey, 1931. Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetailsandid=415516, on 22 May 2012.

Rosenberg, G., F. Moretzsohn, and E. Garcia. 2009. Gastropoda (Mollusca) of the Gulf of Mexico. pp. 579–699. In: D. Felder and S. Earle. Gulf of Mexico origin, waters and biota: biodiversity. Texas A&M University Press, College Station, 1312 pp.

Santos, F.N., C.H.S. Caetano, R.S. Absalão, and T.S. De Paula. 2007. Mollusca de substrato não consolidado. pp. 207–236. In: J.C. Creed, D.O. Pires and M.A.O. Figueiredo (eds). Biodiversidade marinha da Baía da Ilha Grande. Ministério do Meio Ambiente, Brasília, 416 pp.

Simone, L.R.L. 2006. A new Triphoridae from Canopus Bank, N.E. Brazil (Caenogastropoda). Strombus 13(1): 6–8.

Smith, E.A. 1890. Report on the marine molluscan fauna of the island of St. Helena. Proceedings of the Zoological Society of London 1890: 247–317, pls. XXI–XXIV.

Tavares, M. 1999. The cruise of the Marion Dufresne off the Brazilian coast: account of the scientific results and list of stations. Zoosystema 21 (4): 597–605.

Tunnell, J. W., J. Andrews, N. C. Barrera, and F. Moretzsohn. 2010. Encyclopedia of Texas seashells – identification, ecology, distribution and history. Harte Research Institute for Gulf of Mexico Studies Series, College Station, XI + 512 pp.

Vokes, H. E. and E. H. Vokes. 1983. Distribution of shallow-water marine Mollusca, Yucatan Peninsula, Mexico. New Orleans, Mesoamerican Ecology Institute, Middle American Research Institute, VIII + 183 pp.

Warmke, G.L. and R.T. Abbott. 1962. Caribbean seashells. New York, Dover Publications, XX + 348 pp.

Wilson, B. 1993. Australian Marine Shells – Prosobranch Gastropods, Part 1. Odyssey Publishing, Kalaroo, 408 pp.

Diel variation affects estimates of biodiversity and abundance of nudibranch (Gastropoda) faunas

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ABSTRACT

With approximately 3000 species worldwide, the Nudibranchia is numerically the largest group of sea slugs (Gastropoda: Heterobranchia). In most previous surveys on diversity and abundance of nudibranch faunas, researchers only undertook daytime surveys and neglected nighttime surveys for practical reasons. In order to assess whether such estimates are accurate if they are based only on daytime surveys, we undertook replicated diel (i.e., day and night) surveys for 12 consecutive months (from December 2009 to November 2010) at Shilang Marine Reserve, Green Island (Lyudao), Taiwan. We analyzed the species accumulation curves, diversity indices, and similarity of species composition as statistical estimates of overall biodiversity and species abundance. Fifty-three species of nudibranchs were recorded during all our surveys, but the cumulative number of species showed no sign of reaching a plateau at the end of our survey. We recorded 34 species during the daytime surveys and 42 species during the nighttime surveys. The mean number of species observed during the day and night was 6.3 and 8.9, respectively. *Phyllidiella pustulosa* was the species observed most often during the daytime surveys, while *Tritonia* sp. 1 (an undescribed species) was the most abundant species at night. Species composition was clearly different between day and night. Our results for this particular region of the tropical Indo-Pacific Ocean, which is adjacent to the "Coral Triangle" region of global maximum biodiversity of nudibranchs, lead us to conclude that estimates of faunal diversity and species composition within local communities (richness) are strongly influenced by whether surveys are conducted during the day or the night. Furthermore, regardless of when and how such surveys are conducted in tropical seas, the estimates of biodiversity they produce will inevitably fall far short of total biodiversity.

Additional Keywords: nudibranch, biodiversity, day-night quantitative surveys, Green Island (Lyudao)

INTRODUCTION

The Nudibranchia is the most morphologically complex and ecologically diverse group of the marine Heterobranchia. It comprises about 3000 species worldwide, though probably less than half of them are presently formally named (Wägele and Willan, 2000; Willan, pers. obs.). All nudibranchs are carnivorous, being predators on a wide variety of organisms—sponges, hydrozoans, scleractinian corals, octocorals, scyphozoans, bryozoans, kamptozoans, crustaceans, ophiuroids, ascidians, fishes, and even other sea slugs. Most nudibranchs are highly specialized for feeding on only one particular species of prey item. Therefore, the presence and abundance of nudibranchs may act as a useful indicator of the overall diversity of marine organisms in an ecosystem (Lock et al., 2010). The best way to measure the presence and abundance of nudibranchs is to study their biodiversity both systematically and quantitatively. Biodiversity is the full variety of genetic diversity, species diversity, and ecosystem diversity, which are usually measured by species richness and evenness. Biodiversity is relevant to conservation. Understanding spatial and temporal variation of species composition are important for effective biodiversity conservation strategies (Roberts and Gilliam, 1995).

In terms of the geographical distribution of nudibranchs, the number of species is far greater in the tropical zones of the world than in temperate zones (Table 1), and this conclusion is generally consistent across the

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Table 1. The total number of nudibranch species recorded at different latitudes of the world (arranged from north to south). The dashed lines separate the temperate and subtropical/tropical faunas. The data for number of species includes both described and undescribed species.

Locality	Average latitude	Number of species	References
Greenland (unknown)	72° N	24	Jensen, 2005
Iceland (unknown)	65° N	41	Jensen, 2005
Faroe Islands (8 years)	62° N	38	Jensen, 2005; Sneli et al., 2005
Alaska (unknown)	61°35′ N	63	Jensen, 2005
Skomer, Wales (35 years)	51°44′ N	72	Lock et al., 2010
Baja California, Mexico (40 years)	34°23′ N	117	Bertsch, 2010
Ryu-Kyu (50 years)	26°30′ N	435	Ono, 2004
Bahía de Banderas, Mexico (9 years)	20°40′ N	111	Hermosillo-González, 2011
Taiwan (7 years)	23°30′ N	588	Chang et al., 2012 (unpublished)
Mariana Islands (42 years)	17°00′ N	238	Carlson and Hoff, 2003
Marshall Islands (20 years)	11°18′ N	432	S. Johnson pers. comm.
Philippine Islands (5 years)	13°00′ N	> 800	Poppe, 2010; Willan pers. obs.
Northern Great Barrier Reef, Australia (6 years)	14°40′ S	94	Wägele et al., 2006
Fiji (4 years)	18°10′ S	162	Brodie and Brodie, 1990
New Caledonia (10 years)	21°10′ S	348	Hervé, 2010; Hervé pers. comm.
Southern Great Barrier Reef, Australia (32 years)	23°27′ S	197	Marshall and Willan, 1999
Sunshine Coast, Australia (8 years)	26°40′ S	381	Cobb et al., 2012
Victoria, Australia (52 years)	39°15′ S	230	Burn, 2006
New Zealand (50 years)	41° S	100	Spencer et al., 2011

globe. However, latitude alone does not completely explain global biodiversity as some regions in the tropical Indo-Pacific Ocean (in particular the "Coral Triangle") have biodiversity of nudibranchs orders of magnitude higher than other tropical regions such as the Caribbean Sea and tropical western Africa (Gosliner et al., 2008).

This information on large scale biodiversity and presence of species within local communities (richness) in nudibranch faunas are accumulating gradually, particularly so for the megadiverse "Coral Triange" region and the regions immediately adjacent to it such as the South China Sea, Melanesia, Micronesia, and tropical northern Australia. What is emerging already is that estimates of biodiversity and species richness are heavily reliant upon the way the data are collected, both temporally and spatially. Several factors affect the occurrence of species and hence their chance of being recorded – sampling effort and technique, experience of the investigators (in particular their "search image" for cryptic and microscopic species), season, time of day, environmental conditions (such as surge), and the heterogeneity of the habitat itself. As one example of such a quantitative survey, we cite Johnson's (1983) pioneering study of two species of nudibranchs (i.e., the species that he called *Chromolaichma youngbleuthi* (Kay and Young, 1969) (presently *Glossodoris rufomarginata* (Bergh, 1890)) and *Hypselodoris* sp. 1 (presently *Hypselodoris peasei* (Bergh, 1880)) on the subtidal reef at Hawaii where he found that the number of individuals was not stable throughout the year. Furthermore, the actual duration of the survey is very important to the final estimate of biodiversity. The longer the sampling period, the more the cumulative number of species will increase, but this increase is only very gradual as nudibranchs are inherently rare in time and space (Marshall and Willan, 1999). For example, Gary Cobb (pers. obs.) and his colleagues have presently recorded 381 species of nudibranchs in the same area in southern coastal Queensland (Table 1), yet even more importantly, even after eight years of continuous (i.e., weekly) surveying, they are still discovering further species at an average of 1.18 additional species every week.

Since nudibranchs are rather slow-moving animals, one does not expect them to show strong daily patterns of activity; one assumes all species are always present and always visible, and this assumption underlies surveys for biodiversity and richness. However, careful observations made *in situ* underwater show that some species do, in fact, possess daily patterns of (feeding and locomotor) activity; Bertsch and Johnson (1981: 66, 107) and Johnson (1983: 3; 1989) report that one species of *Hypselodoris* (presently known as *H. peasei*) in Hawaii was observed during the day crawling or feeding in groups of up to 30 or more individuals (its colloquial name being "locust") on its specific sponge food (*Luffariella* sp., family Thorectidae). However, just before sunset all the individuals left their food sponge and moved one after the other into a nearby crevice where they hid for the night. This is an example of a diurnal (i.e., day-active) species. Conversely, some species are reported as exclusively nocturnal (Johnson 1989; Behrens, 2005: 20, 142; Holland, 2008), for example the tropical Hawaiian dorids *Chromodoris* sp., *Aldisa pikokai* Bertsch and Johnson, 1982 and *Sclerodoris paliensis* Bertsch and Johnson, 1982 (Johnson, 1989). In our experience working with temperate and tropical Pacific nudibranch faunas, the "classic" group of nocturnal

nudibranchs comprises members of the genus *Janolus* (family Zephyrinidae), all of which are cryptic. During the day, individuals hide deeply within the arborescent Catenicellidae bryozoans, on which they feed. They are truly impossible to find. But at night they emerge to graze on the tips of these bryozoans and are quite conspicuous (Miller and Willan, 1986).

Our study, conducted in southeastern Taiwan, investigates such temporal variation quantitatively by comparing the composition of the nudibranch fauna by day and by night, and season by season, and it investigates quantitatively how predictive such a survey is for estimation of overall nudibranch biodiversity at one particular locality. In Taiwan, the only similarly rigorous precursor is that by Su et al. (2009). These workers, all of whom were "amateur" nudibranch researchers, undertook 17 consecutive monthly surveys during the daytime at the Pescadores Islands (Penghu) off the west coast of the mainland. They concluded that species composition showed no obvious pattern between seasons or months.

MATERIALS AND METHODS

Study Site: Taiwan is a large island located in the tropical Western Pacific Ocean bathed by the Kuroshio Current that originates southeast of the Philippine archipelago and flows northward to Japan. The Kuroshio branches south of Taiwan. The major branch goes through the Philippine Sea past the eastern coast of Taiwan, and the weaker branch goes through the Taiwan Strait past the western coast of Taiwan. The Kuroshio Current is characterized by high water temperature, high salinity and low nutrients (Chen et al., 1994), physical parameters most favorable for the development of coral reefs. Green Island (Lyudao), a small remnant volcano located southeast of the Taiwanese mainland, lies in the path of the main branch of the Kuroshio Current. Uniquely for Taiwan, the study site at Shilang on the eastern coast of Green Island (22°39.37′ N, 121° 27.45′ E) has numerous coral reefs and coral patches (Figure 1), and since 2003 has been declared a marine fishery reserve. Since then, all types of fishing have been forbidden. Shilang is also an ideal site for a full-year survey due to its fortuitous geographic location—in winter the strong northeastern monsoon is blocked by the central chain of mountains on Green Island, and in summer Shilang is sheltered from the southern monsoon because it is on the western coast of Green Island. The seas are generally calm year round.

Field Survey Methods: During the period between December 2009 and November 2010, we undertook 12 consecutive monthly diel surveys of nudibranchs by scuba diving at Shilang. All of the surveys were conducted using shore-entry and the divers had to walk about 30 meters across the rocky intertidal zone carrying their scuba gear to access the water. Therefore, for safety monthly surveys were always timed when the seas were calmest. Most of the surveys were conducted during periods of complete calm with low waves, but some months there was a strong surge under water.

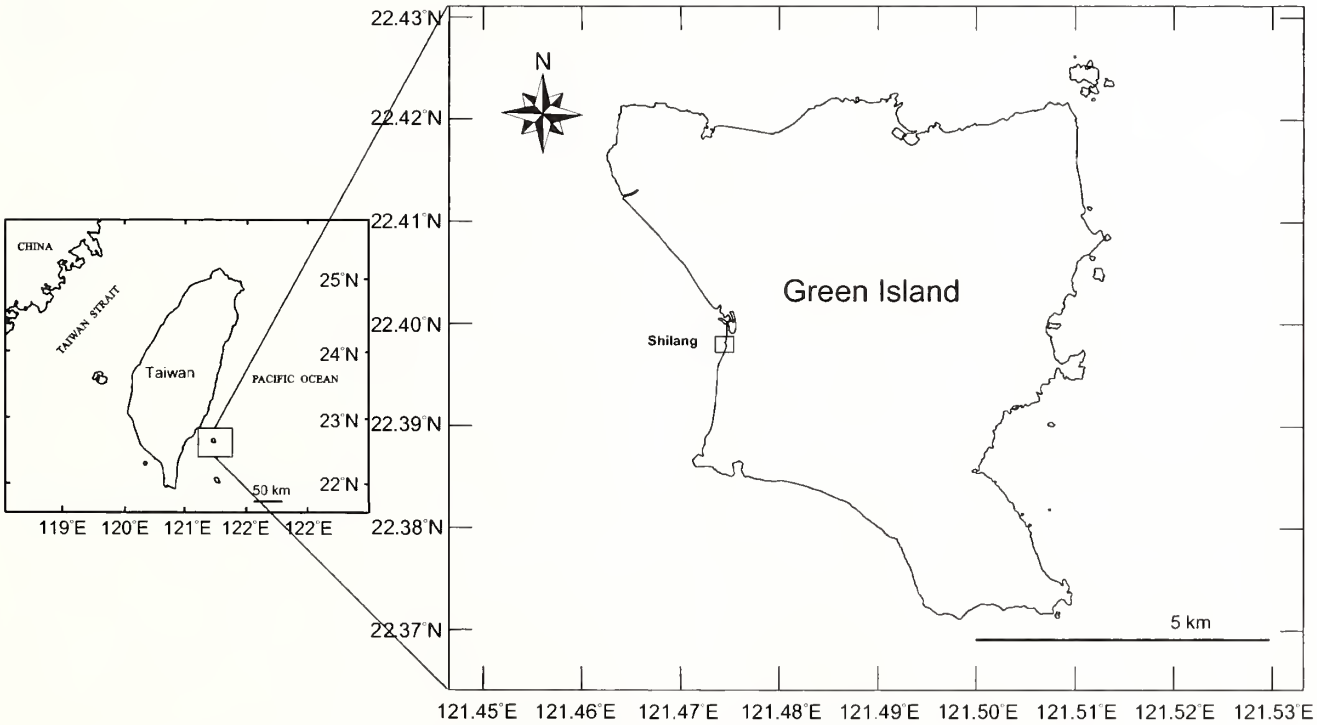
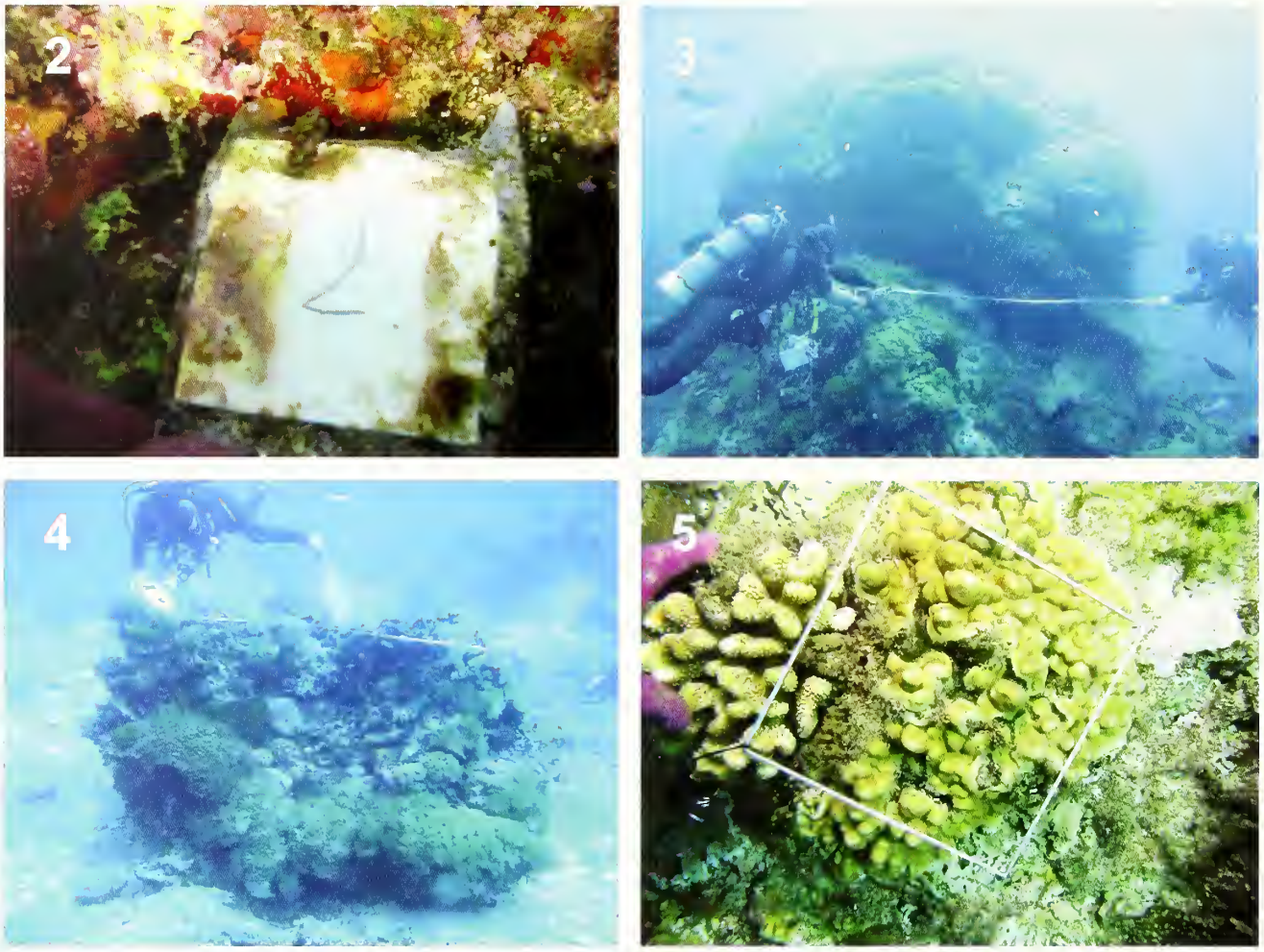


Figure 1. Map showing the location of Green Island off the southeastern coast of Taiwan. The enlargement on the right indicates the study site at Shilang (22° 39.37′ N, 121° 27.45′ E).



Figures 2–5. Techniques used for data collection at the study site: **2.** One of the individually marked rocks (rock number 2). **3–4.** Divers using a 2 m tape to measure a marked rock. **5.** Detail of habitat recording using a 20 × 20 cm quadrat.

In order to study species composition systematically, we marked eight rocks (Figure 2), within a total area of 600 m^2 (i.e. a rectangle 30 m in length from shore by 20 m width) prior to the commencement of our survey. On our survey transect we always swam straight out to the farthest rock (no. 8) and started the survey there allowing approximately 70 minutes for each survey. On each monthly dive, two divers searched thoroughly around the marked rocks. One diver (the senior author of this paper) recorded all species and individuals and took photographs of them all. His buddy diver (the fifth author of this paper) was assigned to take photographs and search for nudibranchs in caves. All recordings were written on waterproof paper. All our surveys were conducted in depths shallower than 12 m. On each occasion, seawater temperatures were recorded in dive computers (Suunto Mosquito). To avoid disturbance and to conform to the conservation status of the Shilang Marine Reserve, neither diver collected any specimens on these survey dives. Waterproof torches (Saekodive AL-29) were used at night. We delayed night dives until after 20 hr because of previous observations that nocturnal nudibranchs did not emerge until then.

Habitat Analysis: In October 2011, prior to the start of the quantitative survey for nudibranchs, we measured the height, length, and width of each of the eight study rocks by taking a photograph with a 2 m measuring tape as a scale (Figures 3, 4). Measurements were computed by Image J software (1.43u, National Institutes of Health, USA). At the same time, we also undertook a quantitative description of the habitat types on each rock. We placed a 20 × 20 cm quadrat frame (Figure 5) randomly on 10 sites on each rock and took a photograph of each quadrat using Vidana 1.0.1 beta software. It should be noted that the cover of algae was particularly low at that time of year because it was late autumn. We observed that the algae at this site have an annual fluctuation, with a bloom during spring to summer and a reduction in density and composition during winter. We analyzed 10 photographs on each rock using Vidana 1.0.1 beta software. Descriptive information for the eight study rocks is given in Table 2.

Table 2. Comparison of habitats sampled (eight separate rocks) and type of habitat. The proportion of each habitat type (and percent cover) are given for each of the four habitat types.

	Rock size	Habitat type (cm^2)			
Rock No.	length (m)×width (m)×height (m)	Algae	Coral	Sponges	Bare substrate and others
1	3.7×3.2×4.0	541.02 (13.5%)	2763.28 (69.2%)	376.56 (9.4%)	312.5 (7.8%)
2	3.2×3.1×4.0	498.83 (12.5%)	2668.49 (66.8%)	253.51 (6.3%)	572.66 (14.3%)
3	3.9×3.6×2.3	1143.48 (28.6%)	2235.16 (55.9%)	339.84 (8.5%)	278.52 (7.0%)
4	3.7×2.9×1.8	658.35 (16.5%)	1757.81 (44.0%)	710.16 (17.8%)	866.02 (21.7%)
5	2.8×1.9×1.2	226.17 (5.7%)	2522.84 (63.3%)	458.38 (11.5%)	779.69 (19.6%)
6	4.8×2.9×2.9	62.11 (1.6%)	3284.38 (82.3%)	306.64 (7.7%)	336.33 (8.4%)
7	3.4×3.1×0.8	60.55 (1.5%)	3727.34 (93.2%)	132.81 (3.3%)	78.91 (2.0%)
8	5.5×2.3×4.0	326.17 (8.2%)	3210.17 (80.3%)	261.72 (6.5%)	199.61 (5.0%)

Species Identification and Cumulative Curve: The third author identified every individual from the photographs taken during the surveys. All individuals were identified. After the identification process, we created the data matrix with the sample time in rows and the species in columns in an Excel spreadsheet (**Appendix 1.** Matrices of species composition data for the day and night surveys at the study site at Shilang, Green Island, Taiwan, posted at http://nautilus.shellmuseum.org). The species cumulative curves were plotted based on samples and individuals for the diel surveys. Rarefaction curves, an analytical method representing re-sampling of all individuals, showed smoothed cumulative number of species obtained per sample (Gotelli and Colwell, 2001). We used EstimateS version 8.2.0 (Colwell, 2009), which computed rarefaction curves based on the samples.

Biodiversity Index and Species Similarity: In order to compare the species richness and richness between the day and night surveys, we used the Shannon-Wiener H′ Diversity Index (Pielou, 1975) for species richness: $H' = -\sum_{i=1}^{s} (Pi \ln Pi)$, where Pi is the proportion of individuals of each species to the total number of individuals. Pielou's Evenness Index was used for assessing species evenness (Pielou, 1966): $J=H'/H'_{max}$, where H′ is Shannon-Wiener H′ Diversity Index, H'_{max}=the maximum of Shannon-Wiener H′ diversity indexes. To compare the species composition of the diel surveys, we log transformed the number of individuals and used the Bray-Curtis Coefficient to estimate the similarity. A dendrogram was constructed using the unweighted pair-group clustering method using arithmetic averages (UPGMA clustering method) (Romesburg, 1984). All the biodiversity and species similarity data were computed by the Primer 6.0 software package (Clarke and Gorley, 2006).

Statistical Analyses: To compare the number of species, number of individuals, Shannon-Wiener H′ Diversity Index and Pielou's Evenness Index between day and night, we used the Wilcoxon Signed Ranks Test to compare the two sets of data that were arranged in the Microsoft Excel spreadsheet. We also used the Kruskal-Wallis Test to compare abundances between the seasons for soft coral-feeding and sponge-feeding groups of nudibranchs, i.e., Tritoniidae and Chromodoridae plus Phyllidiidae, respectively.

RESULTS

Habitat Analysis: The habitat types dominating the eight rocks at our study site at Green Island (Lyudao) were algae, (hard plus soft) corals, sponges and bare rock surfaces. Detailed information about the habitats themselves is given in Table 2. Among the rocks, most had a high percent cover of coral, ranging from 44.0 to 93.2 %. The percentage cover of algae ranged from 1.5 to 28.6 %. As mentioned above, it was possible that the lowest percentage of algae (1.5 %) was because the date chosen to record the habitats was in late autumn (31 October 2011) and also because the particular rock (number 7) on which this lowest algal cover recorded was located in relatively deep water. For sponges, the percentage cover ranged from 3.3 to 17.8 %. For bare substrates, the percentage cover ranged from 2.0 to 21.7 %.

Species Identification and Cumulative Curve: Over the year of the survey, we recorded a cumulative total of 53 species of nudibranchs (13 families) including six possible new species. Thirty-four species (10 families) were recorded during the day and 42 species (13 families) at night. The mean number of species recorded for each

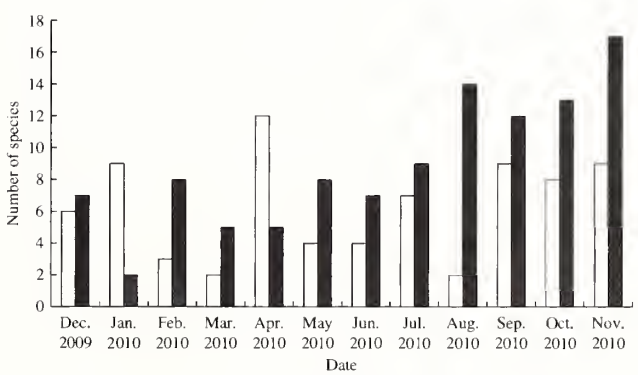


Figure 6. Number of species for all surveys. □ represents daytime surveys. ■ represents nighttime surveys.

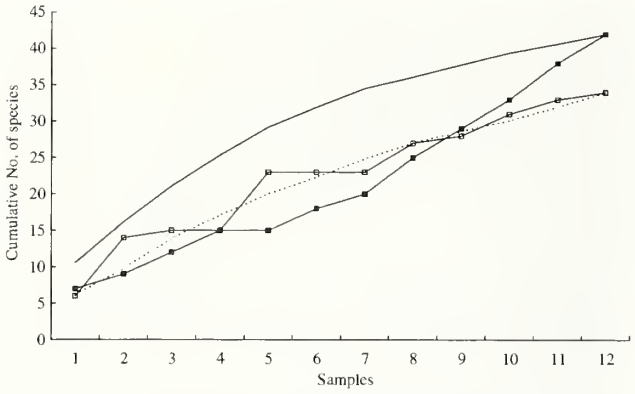


Figure 7. Relationship between the cumulative number of species and monthly samples taken during all surveys. □ represents daytime surveys. ■ represents nighttime surveys. ..... represents daytime rarefaction. —— represents nighttime rarefaction.

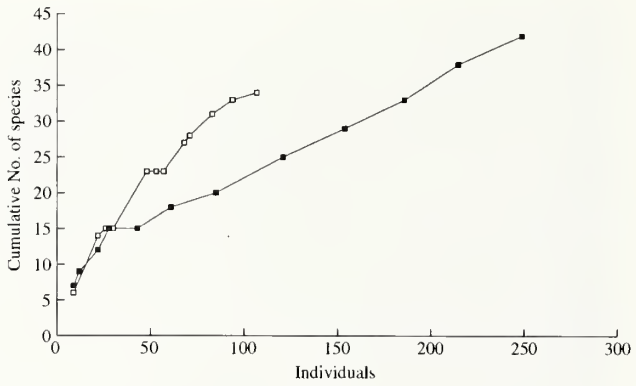


Figure 8. Relationship between the cumulative number of species and individuals sampled during all surveys. □ represents daytime surveys. ■ represents nighttime surveys.

monthly survey was 6.3 during the day (range 2–12 species) and 8.9 species during the night (range 2–17 species) (Figure 6). There was no significant difference in the actual number of species between the day and the night (Wilcoxon Signed Ranks Test, df = 11, N = 12, P = 0.116). The mean number of individuals recorded for each monthly survey was 8.9 individuals during the day (range 4–18 individuals) and 20.2 individuals during the night (range 3–36 individuals). The number of individuals observed at night was significantly higher than during the day (Wilcoxon Signed Ranks Test, df = 11, N = 12, P = 0.016).

The highest number of species of nudibranchs we recorded during the day was 12 species in April 2010. The highest number of species we recorded during the night was 17 species in November 2010. The lowest number of species we recorded during the day was two species in March and August 2010. The lowest number of species we recorded during the night was two species in January 2010.

The sample-based cumulative curves showed 34 species were recorded during the day versus 42 species at night (Figure 7). The figure for diversity had still not reached a plateau after 12 months, which means that even after twelve surveys (i.e., 24 collections of data) some species had still not been observed. In the sample-based rarefaction curves, the daytime curve was a good match for its rarefaction curve. However, the nighttime curve was far removed from its rarefaction curve (Figure 7). Rarefaction curves were used to randomize all the species in all the samples. If the cumulative curve was much lower than the rarefaction curve, it represented the aggregation of species during the samples. On the individual-based cumulative curve, more individuals were recorded at night and the slope obviously showed the species did not reach a plateau (Figure 8).

Across all our surveys, the number of individuals recorded at night was consistently greater than that for the day except for December 2009, January 2010 and April 2010. The highest number of individuals during the day was 18 individuals in April 2010 and during the night it was 36 individuals in July 2010. The lowest number of individuals during the day was three individuals in August 2010 and during the night it was three individuals in January 2010. We counted a total of 107 individuals during the day and 249 individuals at night across all surveys. The statistical analysis showed that the number of individuals recorded at night was higher than during the day. The main factor responsible for this skew that affects the analysis was the appearance of *Tritonia* sp. 1 during the night. We recorded 111 individuals of this species at night, however only two were recorded during the day across all surveys.

Biodiversity Index and Species Similarity: The Shannon-Wiener H′ Diversity Index showed no clear pattern between day and night surveys (Figure 9) and the statistical results confirmed there was no significant difference between day and night (Wilcoxon Signed Ranks Test, df = 11, N =12, P = 0.433). Pielou's Evenness Index showed a lower value at night than during the day from April to August (Figure 10). This is because large numbers of *Tritonia* sp. 1 appeared and aggregated at night, which produced a lower value of evenness. There was no significant difference in Pielou's Evenness Index between day and night samples (Wilcoxon Signed Ranks Test,

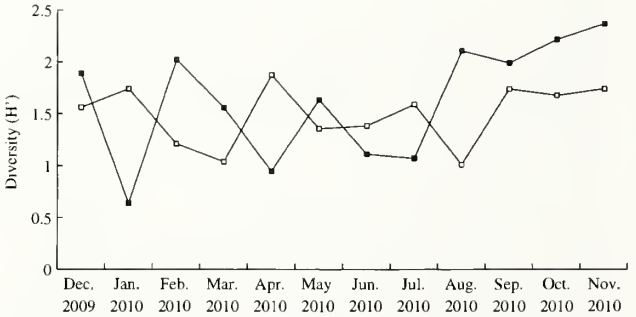


Figure 9. Shannon-Wiener H′ Diversity Index for all surveys. □ represents daytime surveys. ■ represents night time surveys.

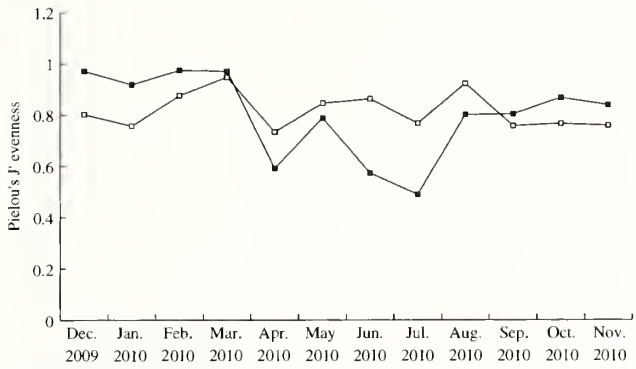


Figure 10. Pielou's Evenness Index for all surveys. □ represents daytime surveys. ■ represents nighttime surveys.

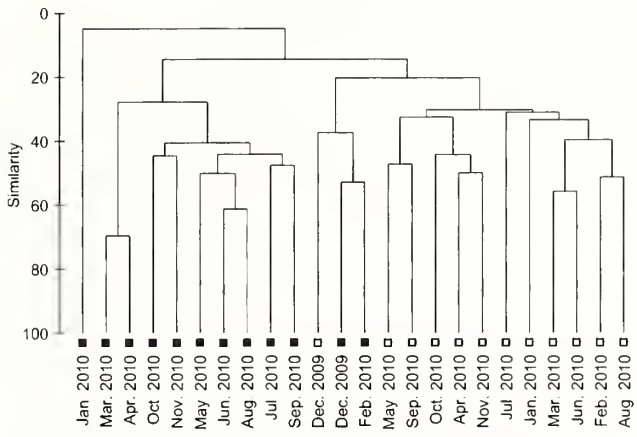


Figure 11. Dendrogram for hierarchial clustering of all surveys (12 months with daytime and nighttime surveys), using group-average linking of Bray-Curtis Coefficient. □ represents daytime surveys. ■ represents night time surveys.

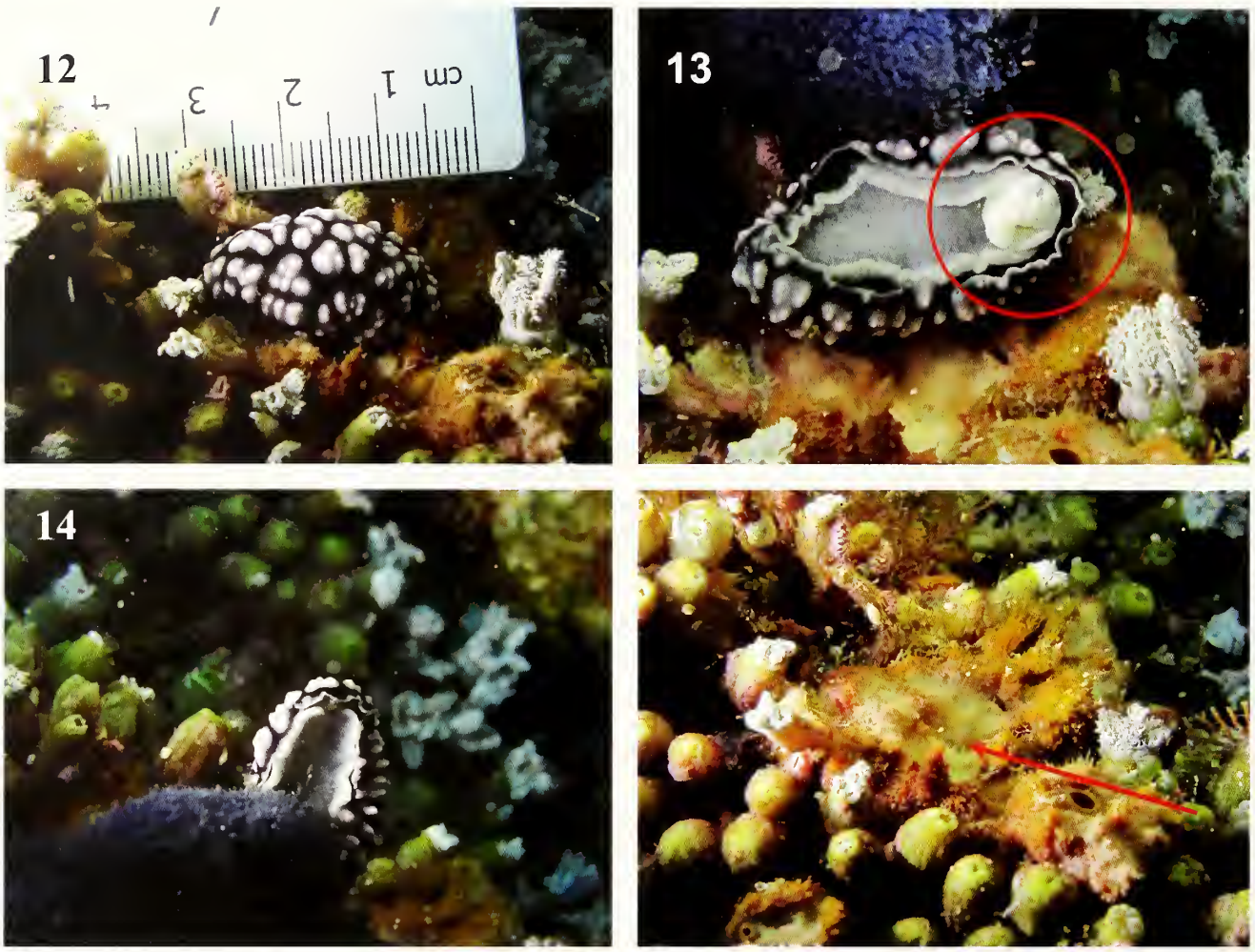
df = 11, N =12, P = 0.875). The analysis dendrogram for hierarchial clustering showed the species compositions between night and day were different (Figure 11). Most of the species recorded during the day and the night formed separated groups, except for two night surveys in December 2009 and February 2010, during which the most frequently recorded nudibranchs belonged to the family Phyllidiidae. However, there was no clear pattern between months and seasons (Figure 11). The most frequently recorded species overall was *Phyllidiella pustulosa* (Cuvier, 1804) (Figures 12–15). It appeared 17 times during 24 surveys (12 months at daytime and 5 months at nighttime). The most abundant species overall was *Tritonia* sp. 1 (Figure 16), which was recorded 11 times during 24 surveys (one month at daytime and 10 months at nighttime). In terms of abundance, 111 individuals of *Tritonia* sp. 1, were recorded at night and only two individuals were recorded during the day. Most of them were recorded on rock number eight on top of the octocoral *Tubipora musica* Linnaeus, 1758 (family Tubiporidae) (which is their food source) and the alga *Caulerpa serrulata* (Forsskål) J.Agardh, 1837 (Figure 17). During the field surveys, we were amazed how cryptic this species was despite it being so common; we found that even on the same coral patch, we could not find any *Tritonia* sp. 1 in the afternoon but a few hours later at night, we recorded numerous individuals. Some of them were mating on the top of the *Tubipora musica* (Figure 18), while others were aggregated on the adjacent bare rock (Figure 19).

As no nudibranchs feed on algae, we used soft coral feeders (Tritoniidae) and sponge feeders (Chromodoridiidae plus Phyllidiidae) to study the relationship between seasons and abundances. The abundance of the sponge feeders was not significantly different between the four seasons (Kruskal-Wallis Test, df = 3, N = 12, P = 0.08). The average number of individuals in winter and autumn (10.7 and 12.7, respectively) was higher than spring and summer (5.3 and 5.7, respectively). However, the abundance of the soft coral feeders was highly significantly different between the four seasons (Kruskal-Wallis Test, df = 3, N = 12, P = 0.03). The summer had the highest average number of individuals (29.3), followed by autumn (27.7), and spring (12.2). In winter, we recorded the lowest average number of individuals (3.7). The sponge feeders were more abundant in winter and autumn. In contrast, the soft coral feeders were more abundant in summer and autumn.

DISCUSSION

Comparing the number of species recorded during the day versus during the night over the entire twelve months of the survey, we found that those recorded during the day were numerically greater than those at night on only two occasions (January 2010 and April 2010), whereas the number of species recorded at night was greater than during the day on ten occasions. However, the statistical analysis showed that the average number of species was not significantly different between the day and the night.

As explained above, we had marked eight rocks from near the shore to some distance offshore. The most visible difference to us between these rocks between the day and the night was the appearance at night of larval fish that aggregated in front of the torch, in addition to nocturnally active crustaceans and polychaetes. Fewer nudibranchs were recorded on the surveys when there was a strong surge (January 2010 night, March 2010 day, and August 2010 day), confirming the observations noted anecdotally at other locations (see Introduction). During all our surveys, the visibility was always greater than 10 m because Green Island was bathed by the clear Kuroshio Current and there are no rivers on the island that would introduce terrigenous silt into the marine environment and reduce visibility. The only occasions when visibility dropped significantly were after typhoons. The coral cover was stable during the whole year. The algal density was higher in the spring and summer, and lower during autumn and winter as noted above. During

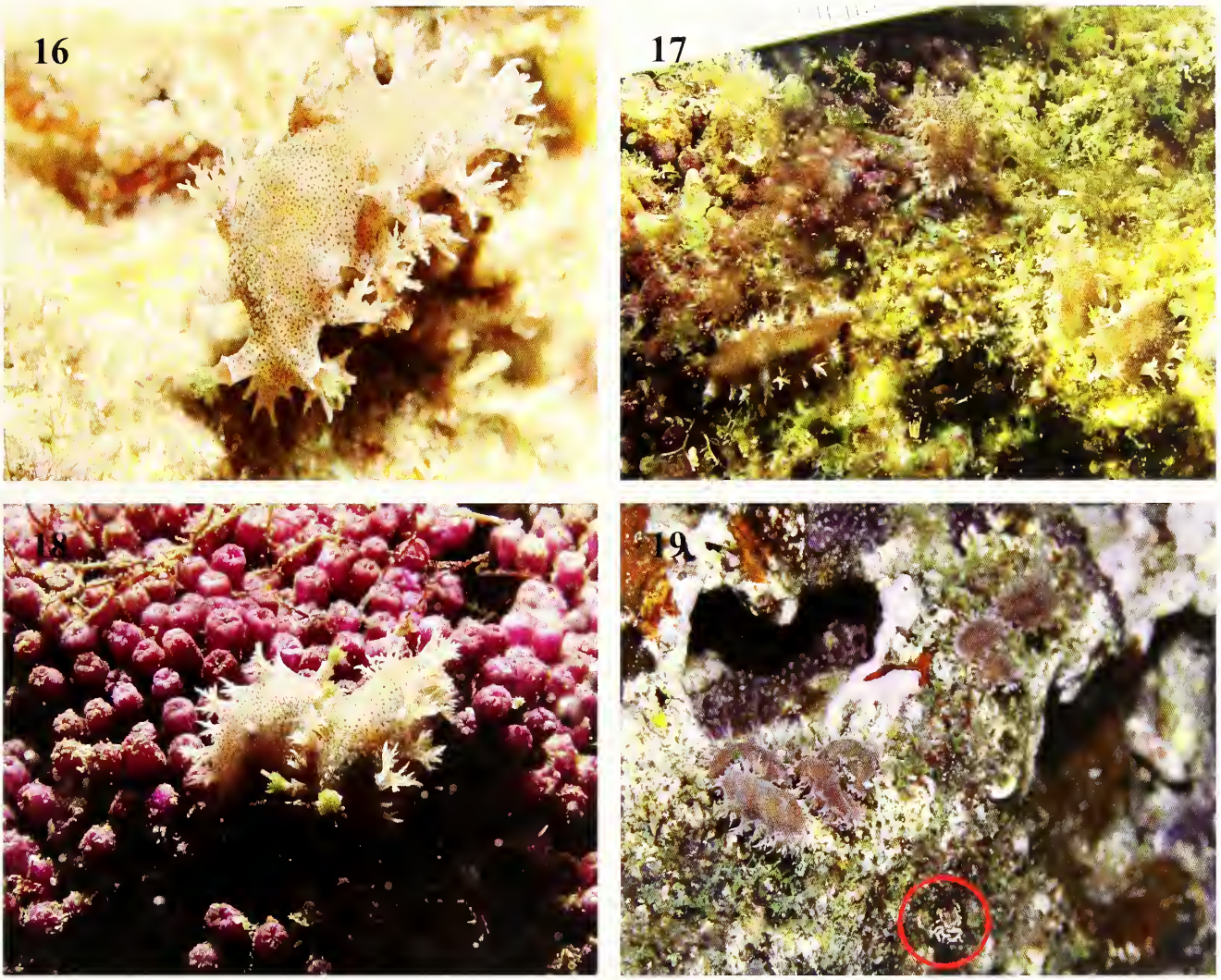


Figures 12–15. The most commonly recorded species during our survey, *Phyllidiella pustulosa*, and its habitat. All photographs taken during the day. **12.** Individual feeding on its food sponge. **13.** Same turned over showing its oral tube everted (circled). **14.** Individual then quickly retracted its oral tube; **15.** The feeding scar left by this individual on the sponge (arrowed). All photographs by the senior author.

the surveys, we recorded more phyllidiids during the day (55 individuals cumulatively) than during the night (30 individuals cumulatively). However, some species were recorded more frequently during the night, e.g. 111 individuals of *Tritonia* sp. 1 were recorded during the night in comparison to two individuals during the day. This species was obviously active during the night.

In a broader view, there are several factors that affect the recording of the cumulative number of species of nudibranchs at a particular locality. The first is latitude; tropical regions support far higher numbers of species than temperate regions (Table 1). The second is survey effort; the longer the period of the survey, the greater the cumulative number of species will be. Our study showed that the number of species had still not reached a plateau even after one year. In fact, records accumulated for Taiwan over a decade reveal the biodiversity of nudibranchs to be over 580 species (pers. observ.), so we only recorded less than 10% of the total fauna. This very gradual accumulation of species is consistent with what is known from nudibranchs elsewhere (e.g., Heron Island, Great Barrier Reef). The third is the time of the survey; most of the previous surveys were conducted in the day which may neglect the nocturnal species. Searches conducted over a long period only in daytime may never record some strictly nocturnal species. The last factor is search experience (i.e. acquiring a "search image"); with time, observers gradually improve their recording skills as they become more adept at seeing cryptic species, and at recognizing small juveniles and species less than 5 mm long.

There was no obvious pattern in the Shannon-Wiener H″ Diversity Index during all our surveys. In Pielou's Evenness Index, most of the months showed that the night data were higher than the day except for the period from April to August 2010. During these five months, we recorded at least nine individuals of *Tritonia* sp. 1. July 2010 had the lowest value because 27 individuals of



Figures 16–19. *In situ* photographs of *Tritonia* sp. 1 and its habitat, all taken at night. **16.** Individual showing its gill plumes and finger-like oral tentacles. **17.** Four individuals aggregated on the habitat. **18.** Two individuals mating on top of the habitat; **19.** An aggregation of eight adult individuals. Note the presence of an individual of the aeolid nudibranch *Phyllodesmium briareum* (circled) on the bare rock some distance away from the closest *Tritonia* sp. 1. Photographs 16 and 19 by the fifth author. Photographs 17 and 18 by the senior author.

Tritonia sp. 1 were recorded. The species similarity showed that there was no obvious pattern in temporal change (month and season), which agrees with the results of Su et al. (2009). However, when we compared the species composition between day and night, we observed that the composition at night was different to that of the day; all the nocturnal species were clustered together except for December 2009 and February 2010, on which more phyllidiids were recorded than on other night surveys.

We observed the number of individuals of *Tritonia* sp. 1 during the night was different over the years; we recorded one individual from December 2009 to February 2010; 22 individuals from March to May 2010; 58 individuals from June to August 2010; and 30 individuals from September to November 2010. These data indicate this species is most abundant during summer and least abundant during winter. However, percent cover of its food source, *Tubipora musica*, was very stable during all of our surveys. Therefore, further investigations are required to discover the factors that affect the population cycle of this species of *Tritonia*.

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LITERATURE CITED

Behrens, D.W. 2005. Nudibranch behavior. New World Publications, Jacksonville, 176 pp.

Bertsch, H. 2010. Biogeography of northeast Pacific opisthobranchs: comparative faunal province studies between Point Conception, California, USA and Punta Aguja, Piura, Perú. Perspectivas en Malacología Mexicana: 221–259.

Bertsch, H. and S. Johnson. 1981. Hawaiian nudibranchs. Oriental Publishing Company, Honolulu, 112 pp.

Brodie, G.D. and J.E. Brodie. 1990. A checklist of the opisthobranch molluscs of Fiji. Journal of the Malacological Society of Australia 11: 53–60.

Burn, R. 2006. A checklist and bibliography of the Opisthobranchia (Mollusca: Gastropoda) of Victoria and the Bass Strait area, south-eastern Australia. Museum Victoria Science Reports 10: 1–42.

Carlson, C. and P.J. Hoff. 2003. The opisthobranchs of the Mariana Islands. Micronesica 35–36: 271–293.

Chen, C.T.A., C.T. Liu, and S.C. Pai. 1994. Transport of oxygen, nutrients and carbonates by the Kuroshio Current. Chinese Journal of Oceanology and Limnology 12: 220–227.

Clarke, K.R. and R.N. Gorley. 2006. Primer v6: user manual/tutorial. PRIMER-E, Plymouth, England.

Cobb, G., D. Mullins, R.C. Willan, T. Farr, and J. Schubert. 2012. Nudibranchs Sunshine Coast Australia: Indo-Pacific region nudibranchs. http://www.nudibranch.com.au (accessed June 2012)

Colwell, R.K. 2009. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. http://purl.oclc.org/estimates (accessed August 2011)

Gosliner, T.M., D.W. Behrens, and Á. Valdés. 2008. Indo-Pacific nudibranchs and sea slugs. A field guide to the world's most diverse fauna. Sea Challengers Natural History books, etc, Washington, 426 pp.

Gotelli, N.J. and R.K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379–391.

Hermosillo-González, A. 2011. Species list of opisthobranch mollusks for Bahía de Banderas (Jalisco-Nayarit), Pacific coast of México. The Festivus 43(4): 39–58.

Hervé, J. 2010. Guide des nudibranches de Nouvelle-Calédonie: et autres Opisthobranches. Catherine Ledru, Nouméa, 401 pp.

Holland, J.S. 2008. Living Color. National Geographic 213(6): 92–105.

Jensen, K.R. 2005. Distribution and zoogeographic affinities of the nudibranch fauna (Mollusca, Opisthobranchia, Nudibranchia) of the Faroe Islands. BIOFAR Proceedings, Annales Societas Scientiarum Færoensis Supplementum 41: 109–124.

Johnson, S. 1983. Distribution of two nudibranch species on a subtidal reef on the western shore of Oahu, Hawaii. The Veliger 25: 356–364.

Johnson, S. 1989. Temporal patterns of nudibranch mollusk activity on a subtidal Hawaiian reef. The Veliger 32: 1–7.

Lock, K., P. Newman and M. Burton. 2010. Skomer Marine Nature Reserve, nudibranch diversity survey 2010. [Cyngor Cefn Gwlad Cymru] Countryside Council for Wales Regional Report 18: 1–35.

Marshall, J.G. and R.C. Willan. 1999. Nudibranchs of Heron Island, Great Barrier Reef: a survey of the Opisthobranchia (sea slugs) of Heron and Wistari Reefs. Backhuys Publishers, Leiden, 268 pp.

Miller, M.C. and R.C. Willan. 1986. A review of the New Zealand arminacean nudibranchs (Opisthobranchia: Arminacea). New Zealand Journal of Zoology 13: 377–408.

Ono, A. 2004. Opisthobranchs of Ryukyu Islands. Rutles, Tokyo, 304 pp.

Pielou, E.C. 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13: 131–144.

Pielou, E.C. 1975. Ecological diversity. John Wiley, New York, 165 pp.

Poppe, G.T. 2010. Philippine Marine Mollusks. Vol. 3 (Gastropoda Part 3 & Bivalvia Part 1). ConchBooks, Hackenheim, 665 pp.

Roberts, M.R. and F.S. Gilliam. 1995. Patterns and mechanisms of plant diversity in forested ecosystems - Implications for forest management. Ecological Applications 5: 969–977.

Romesburg, H.C. 1984. Cluster analysis for researchers. Lifetime Learning Publications, Belmont, 344 pp.

Sneli, J.-A., T. Schiotte, K.R. Jensen, P.B. Wikander, O. Stockland, and J. Sorensen. 2005. The Marine Mollusca of the Faroes. BIOFAR Proceedings, Annales Societas Scientiarum Færoensis Supplementum 42: 15–176.

Spencer, H.G., R.C. Willan, B.A. Marshall, and T.J. Murray. 2011. Checklist of the Recent Mollusca recorded from the New Zealand exclusive economic zone http://www.molluscs.otago.ac.nz/index.html (accessed December 2011)

Su, Y., L.J. Huang, Y.W. Chang, and H.K. Mok. 2009. Temporal changes in nudibranch composition at a coastal site off Penghu (the Pescadores) in the Taiwan Strait. Zoological Studies 48: 448–459.

Wägele, H., I. Burghardt, N. Anthes, J. Evertsen, A. Klussmann-Kolb, and G. Brodie. 2006. Species diversity of opisthobranch molluscs on Lizard Island, Great Barrier Reef, Australia. Records of the Western Australian Museum Supplement 69: 33–59.

Wägele, H. and R.C. Willan. 2000. Phylogeny of the Nudibranchia. Zoological Journal of the Linnean Society 130: 83–181.

Occupancy of strata of plant height and plant substrate by land snail Gastropoda assemblages at Escaleras de Jaruco, Mayabeque, Cuba

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ABSTRACT

The study was carried out in three low hills (Beluca, La Chirigota, and La Jaula) in the Escaleras de Jaruco-Tapaste-Cheche, Mayabeque province, Cuba. On each low hill, ten fixed quadrats of 3 × 3 m were selected and plant strata were identified (strata I: 0–1m of height; II: 1.01–2 m; III: more than 2.01m) in addition to the substrate of the plants used for most representative species of land snail assemblages. At the three outcrops the lowest stratum (I) of the vegetation presented the greatest values of absolute abundance. During the rainy months, *Chondropoma pictum* was the most abundant species in stratum I followed by strata II and III respectively, while during the less rainy months this species was only observed in strata I and II. *Helicina aspersa*, *C. auberianum*, *Jeanneretia bicincta*, and *Zachrysia auricoma* were observed in strata I and II during both rainy and less rainy periods. The branches and trunks contained higher species abundance and frequency of individuals than leaves, which was true of all the species with the exception of *J. bicincta*. Individuals frequency on the upside or downside surface of leaves was very variable. Some species showed small differences in the percentage found on both sides of a leaf (*H. aspersa* and *Z. auricoma*) and other ones showed larger differences (*Zonitoides arboreus*, *C. pictum* and *J. bicincta*).

Additional Keywords: Vegetation, low hills, tropical karstic forest, Protected Area

INTRODUCTION

Land snails rank second in number of species in terrestrial ecosystems, being outnumbered only by arthropods (Russell-Hunter, 1983). Land snails are important not only numerically, but also ecologically, because of their role in nutrient cycling as detritivores, herbivores, and carnivores (Purchon, 1977). Despite their diversity and ecological importance, most of the published information on terrestrial mollusks concerns systematics; relatively little is known about terrestrial molluscan ecology (Álvarez and Willig, 1993). This has improved in recent times with an increase in ecological studies of land snail communities since 2000 (Schilthuizen, 2011).

The majority of current papers dealing with habitat preferences and distribution of terrestrial mollusks concentrate on large-scale relationships, based on comparisons of molluscan communities from geographically distant regions (Stanisic, 1997; Hermida et al., 2000; Müller et al., 2005; Cameron and Pokryszko, 2007; Stanisic et al., 2007; Correa-Sandoval et al., 2009; Nekola 2002, 2009). Studies on small-scale snail distribution and microhabitat choice were scarce until fairly recently. More recently, many field and experimental studies have examined ecological differences in the relative abundance and species composition of the communities among and between microhabitats (Kozłowski and Kałuski, 2004; Kappes, 2005; Kappes et al., 2006, 2009; Perea et al., 2007; Sołymos et al., 2006, 2009; Čejka and Hamerlik, 2009; Szybiak et al., 2009).

What little knowledge exists on microhabitat choice in Cuban land snail species is based on arboreal species. The majority of studies have been on charismatic species and populations; examples are Bidart and Espinosa (1989) on *Polymita picta nigrolimbata* Torre, 1950, *Coryda alauda* (Férussac, 1821) and *Caracolus sagemon rostrata* (Pfeiffer, 1847); Bidart et al. (1992) y Fernández et al. (2000) on *Polymita muscarum* (Lea, 1834); Álvarez and Berovides (1989) and Bidart et al. (1992) on *Liguus fasciatus achatinus* Clench 1934; Bidart et al. (1992) on *Hemitrochus lucipeta* (Poey, 1854). The majority of these works are focused on a only a few species. In contrast, this study attempts to examine the entire land snail community by identifying and analyzing the variations of the use of plant height strata and substrate of the plants in a natural Cuban habitat, namely the protected area Escaleras de Jaruco-Tapaste-Cheche (Natural protected landscape), Mayabeque, Cuba.

MATERIALS AND METHODS

The study was conducted in the Escaleras de Jaruco-Tapaste-Cheche Protected Area (23°00′00″ N, 82°01′27″ W; 23°03′27″ N, 82°08′20″ W) which is predominantly a

tropical karstic forest. This park is situated in western Cuba. The area comprises a series of raised limestone outcrops and is a calcareous elevation of Miocene age about 15 km in length, 3–7 km in width, and approximately 300 m a.s.l., where karst funnels, cones, and domes are observed (Cañas and Ysalgué 1978). The study was carried out in three low hills: Beluca, La Chirigota and La Jaula (Figure 1). Tropical karstic forest is the vegetation type present in each elevation. This includes evergreen and/or semi-deciduous forests. At the highest elevations there are thickets with weedy species.

The study was carried out monthly in the period of abundant rains of August to November (November is usually considered a less rainy month, but during this study it behaved like a rainy month) and the less rainy period of January to April 2010. In each locality, ten fixed plots of 3 × 3 m separated by more than 20 m were selected. Within each plot vegetation (branches-trunk and leaves), the land snails were examined only in the sub-canopy. The average of shrubs/trees was eight for plot and 88 % of canopy.

The absolute abundance and the frequency of occurrence (FO) of species were determined. Based

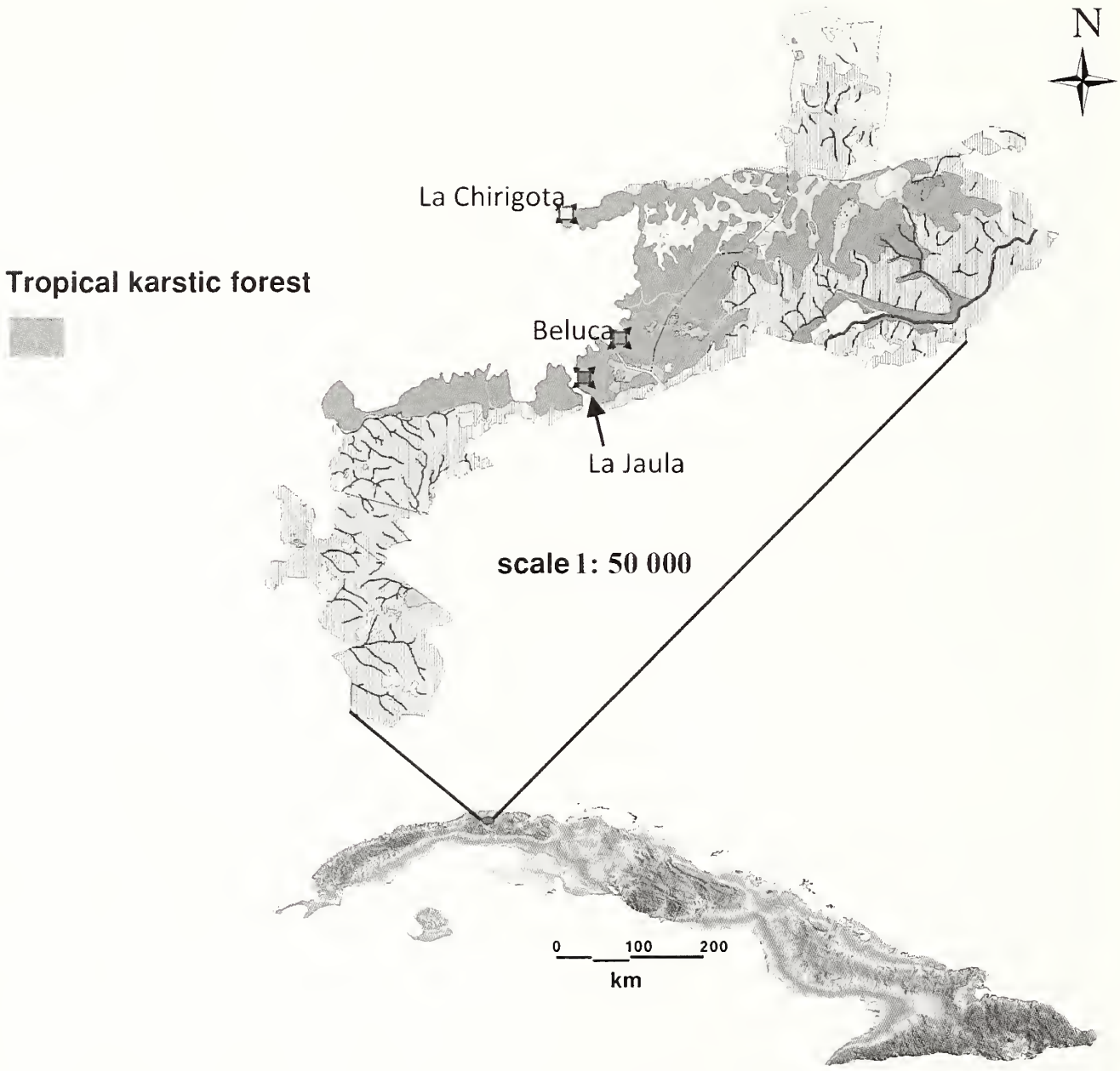

Figure 1. Geographic location of karstic low hills (limestone outcrops) selected for the study of terrestrial arboreal snails of the protected area "Escaleras de Jaruco-Tapaste-Cheche", Mayabeque, Cuba.

on occurrence, the species were classified into one of four arbitrary categories: rare (FO $\leq$ 25 %), occasional (25% < FO $\geq$ 50%), uncommon (50 % < FO $\geq$ 75 %) or common (75 % < FO $\geq$ 100 %). We established three strata (stratum I: 0–1m of height; II: 1.01–2 m; III: more than 2.01m) of the vegetation to analyze vertical distribution of the species. The absolute abundance in the three strata in each elevation and in the most representative species was compared by means of a one-way ANOVA with Tukey HSD test as a post-hoc test. GraphPad Prism 5 was used for these analyses.

RESULTS

Vertical Distribution of the Land Snail Community in Vegetation: In both wet and dry periods, the majority of species were rare (Table 1). In the rainy months, *Chondropoma pictum* was uncommon in Beluca and occasional in La Chirigota and La Jaula, while in the less rainy months it was rare or was not present at La Chirigota. *Jeanneretia bicincta* showed a low frequency in La Chirigota, while in La Jaula this species was occasional in the rainy months. The rest of the species was present in very low frequency but it is pertinent to highlight that *Helicina aspersa* in La Chirigota and La Jaula, and *Zachrysia auricoma* in La Jaula, showed elevated values among the rare species (Table 1).

In the three elevations, the lowest stratum (stratum I) of the vegetation was found to have the highest value of absolute abundance of individuals (Figure 2). In Beluca, abundance did not show significant differences between the three strata, in La Chirigota and in La Jaula strata I and III were different (Figure 2). The absolute abundances of *Chondropoma auberianum* (F (2, 26) = 0.74, P = 0.48, N = 30) and *C. pictum* (F (2, 26) = 2.27, P = 0.12, N = 30) in the three strata showed no significant differences, while for *Helicina aspersa* (F (2, 26) = 3.48, p = 0.04, N = 30), *Jeanneretia bicincta* (F (2, 26) = 5.04, P = 0.01, N = 30) and *Zachrysia auricoma* (F (2, 26) = 3.68, P = 0.04, N = 30), the abundance in the three strata showed significant differences. In *H. aspersa*, strata II and III showed differences, while for the other two species strata I and III were different.

During the rainy months, *Chondropoma pictum* was more abundant at stratum I with 110 individuals followed by strata II and III with 76 and 34, respectively.

Table 1. Occurrence (%) and classification (arbitrary categories) of the species present in the vegetation in three low hills (limestone outcrops) of Escaleras de Jaruco, Mayabeque, Cuba. The general values (independently of the periods) are shown as well as those for Rainy Months and Less Rainy Months.

Species	General (%)	Rainy Months (%)	Less Rainy Months (%)
Beluca			
Alcadia hispida (Pfeiffer, 1839)	4 (rare)	8 (rare)	–
Chondropoma auberianum (d'Orbigny, 1842)	14 (rare)	20 (rare)	8 (rare)
Chondropoma pictum (Pfeiffer, 1839)	30 (occasional)	53 (uncommon)	8 (rare)
Ustronia sloanei (d'Orbigny, 1842)	1 (rare)	3 (rare)	–
La Chirigota			
Chondropoma pictum (Pfeiffer, 1839)	21 (rare)	43 (occasional)	–
Eutudora jimenoi (Arango in Pfeiffer, 1864)	1 (rare)	3 (rare)	–
Emoda submarginata (Gray, 1824)	1 (rare)	3 (rare)	–
Helicina aspersa (Pfeiffer, 1839)	14 (rare)	20 (rare)	8 (rare)
Jeanneretia bicincta (Menke, 1830)	1 (rare)	3 (rare)	–
Microceramus turricola (Pfeiffer, 1839)	1 (rare)	3 (rare)	–
Torrella inmersa (Gundlach in Pfeiffer, 1857)	3 (rare)	5 (rare)	–
Zachrysia auricoma (Férussac, 1822)	3 (rare)	5 (rare)	–
La Jaula			
Alcadia hispida (Pfeiffer, 1839)	4 (rare)	8 (rare)	–
Chondropoma auberianum (d'Orbigny, 1842)	3 (rare)	5 (rare)	–
Chondropoma pictum (Pfeiffer, 1839)	28 (rare)	48 (occasional)	8 (rare)
Eurycampta bonplandi (Lamarck, 1822)	1 (rare)	3 (rare)	–
Helicina aspersa (Pfeiffer, 1839)	11 (rare)	13 (rare)	10 (rare)
Hojeda boothiana (Pfeiffer, 1839)	3 (rare)	5 (rare)	–
Jeanneretia bicincta (Menke, 1830)	15 (rare)	30 (occasional)	–
Liguus fasciatus (Müller, 1774)	4 (rare)	8 (rare)	–
Oleacina straminea (Deshayes, 1819)	3 (rare)	5 (rare)	–
Rhytidopoma nodulatum (Poey, 1851)	1 (rare)	3 (rare)	–
Setipellis stigmatica (Pfeiffer, 1841)	3 (rare)	5 (rare)	–
Torrella inmersa (Gundlach in Pfeiffer, 1857)	5 (rare)	10 (rare)	–
Veronicella sp.	1 (rare)	3 (rare)	–
Zonitoides arboreus (Say, 1862)	3 (rare)	3 (rare)	3 (rare)
Zachrysia auricoma (Férussac, 1822)	11 (rare)	23 (rare)	–

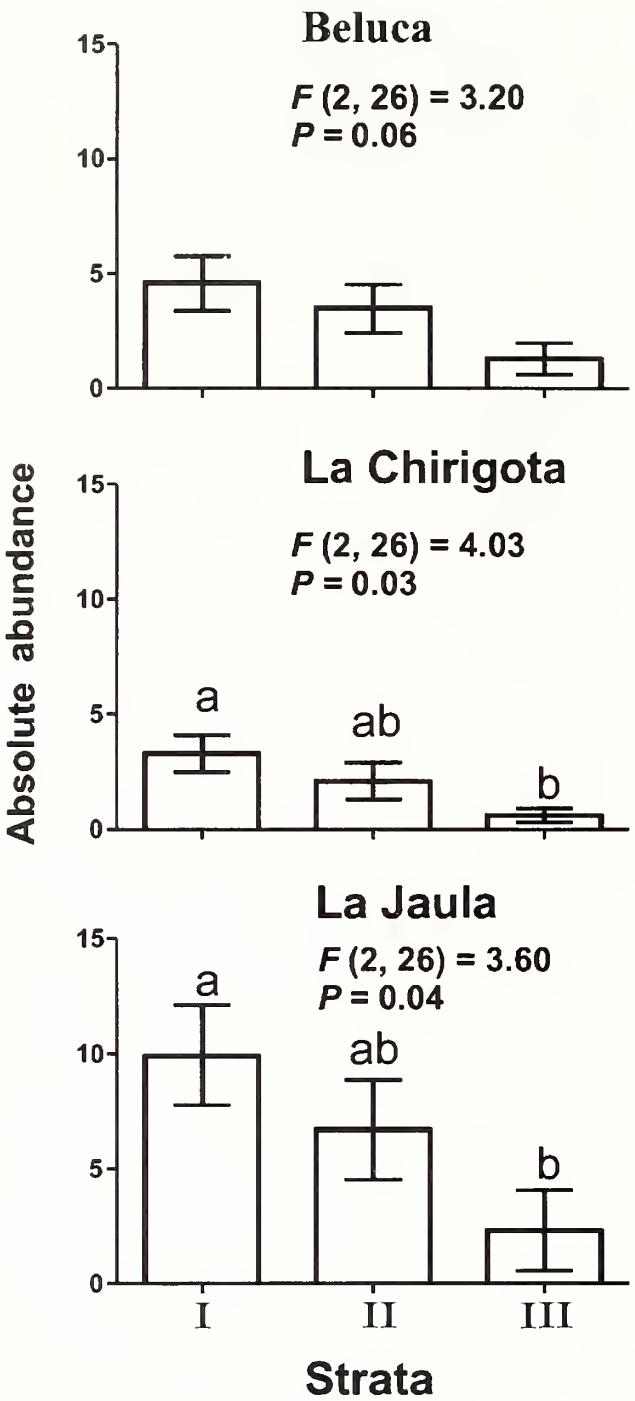

Figure 2. Absolute abundance of land snails in the three strata of vegetation (one: I, two: II, three: III) of three low hills (limestone outcrops) in Escaleras de Jaruco during the 2009-2010. The top of the bar shows the mean and the vertical lines in the shape of "┬" represent the standard error. Letters represent significant differences of abundance between stratums according to the analysis of multiple comparisons (Tukey HSD).

Table 2. Frequency of occurrence (FO) (%) and absolute abundance of the species representative of the tropical karstic forest in three low hills (limestone outcrops) of Escaleras de Jaruco, Mayabeque, Cuba, during 2009–2010.

	Branches-trunk		Leaves	
Species	FO (%)	Abundance	FO (%)	Abundance
Chondropoma auberianum	31	18	3	1
Chondropoma pictum	74	225	8	6
Helicina aspersa	21	14	14	12
Jeanneretia bicincta	0	0	37	16
Zachrysia auricoma	17	6	14	7

However, during the less rainy months, only seven and four individuals of this species were observed in strata I and II, respectively. *Helicina aspersa* was observed with greater abundance during the rainy months in strata I and II, with seven individuals, while only one individual was observed in stratum III; during the less rainy months six individuals were observed in stratum II, four in stratum I and one in stratum III. *Chondropoma auberianum*, *Jeanneretia bicincta*, and *Zachrysia auricoma* were only observed during the period of rainy months in strata I and II.

Use of Vegetative Substrate: Absolute abundance (25 ± 7 SD) and frequency of appearance (41%) of the individuals present in the branches-trunk of vegetation, was higher than abundance (6 ± 1 SD) and frequency of appearance (18 %) in the leaves. This was true of most species (Table 2), with the exception of *Jeanneretia bicincta* that was more abundant and frequent in the leaves.

The appearance of the snail on either the upside or downside surface of the leaves showed variation among the different species. Four species were only observed on the upsides of the leaves (*Eurycampta bonplandi*, *Emoda submarginata*, *Chondropoma auberianum*, *Liguus fasciatus*) and two species only on the downside (*Alcadia hispida*, *Setipellis stigmatica*), each with only one individual. Another six species were observed on both sides of leaves, and *Oleacina straminea* presented one only individual on each side. *Helicina aspersa* (downside, 42 % and upside 58 %) and also *Zachrysia auricoma* (downside, 57 % and upside 43 %) showed little difference in the percentage use of particular leaf sides. In contrast, *Zonitoides arboreus* (downside, 67 % and upside 33 %), *C pictum* (back, 17 % and bundle 83 %) and *Jeanneretia bicincta* (downside, 63 % and upside 37 %) exhibited large percentage differences in the use of particular leaf sides.

DISCUSSION

Determining the use of the environmental resources by land snails is important in supplying information for

a species survival. An essential resource for land snail is food and protective refuges against dehydration (Cook, 2001; Luchtel and Deyrup-Olsen, 2001). To avoid dehydration, their survival depends in large part not only on their behavior, but also on their remarkable ability to tolerate dehydration through suites of physiological mechanisms that help conserve and acquire water (Luchtel and Deyrup-Olsen 2001).

The results of this study reveal perhaps behavioral strategies to minimize dehydration given that the highest abundance was observed in stratum I, primarily in shrubs that are a part of the undergrowth, in which favorable conditions of temperature and relative humidity exist. Low abundance in stratum III of the vegetation may be due to the presence of microclimatic conditions unfavorable for the survival of some of the snails observed in this study. In some other species that inhabit different environments, different behaviors has been described. For example, in semiarid regions, species such as *Cepaea nemoralis* climb up the vegetation, where temperature is cooler, to escape the heat of the ground (Jaremovic and Rollo, 1979). A similar behavior has been observed in *Theba pisana* (Cowie, 1985) and *Liguus fasciatus* (Fernández, 2005), which, during the summer when temperatures increase, use the highest vegetation strata. *Chondropoma pictum* and *Helicina aspersa* (representative species) do not exhibit similar seasonal behaviour since they showed larger values of abundance in strata I and II during the rainy and less rainy months.

Cook (2001) proposes that one such adaptation against dehydration is the use of efficient microhabitats where the risk of dehydration is lower. Nevertheless, the study reveals some differences in species use of vertical strata of vegetation particularly between *Chondropoma pictum*, *Jeanneretia bicincta*, and *Helicina aspersa*. The cause of the low occurrence in this microhabitat is possibly because these species also use rocks and litter as microhabitats, where they can persist with elevated frequency and abundance, perhaps using microhabitats to rest, find refuge, or forage (Hernández, 2011).

Several authors have reported that *Liguus fasciatus* uses strata higher in the vegetation (Fernández, 2005; Álvarez and Berovides, 1989) and this may explain the low observed frequency of this species in the present study, since very high strata may influence a species detectability. Another aspect for consideration is an individual's size; possibly due to the large size of *Liguus fasciatus*, the species may be more susceptible to desiccation in the higher strata of the vegetation than the smaller species. Perrott et al. (2007) demonstrated experimentally that the individuals' size is an important factor in the desiccation stress in the juvenile snails of *Cantareus aspersus* and adults that had smaller shells.

Helicina aspersa, known as an arboreal species (Espinosa and Ortea, 2009), has also been reported in other microhabitats such as rocks and litter (Hernandez, 2011). However, Pérez (1999) observed this species in the vegetation in the locality Hornos de Cal, Sancti Spíritus, in very low frequency (10 %), even with a greater sampling effort. *Chondropoma pictum*, despite being well-represented in the vegetation, is reported by Hernández (2011) as a habitat generalist.

This study found that the majority of the species use trunk-branches, except for *Jeanneretia bicincta*, which is why it is necessary to determine experimentally what induces the use of a determined vegetative substrate. The fundamental use of trunk-branches has been reported for other arboreal Cuban species like *Polymita muscarum* (Fernandez et al., 2000), *Polymita venusta*, *Hemitrochus* sp. (Santos, 2000) and *Liguus fasciatus* (Álvarez and Berovides, 1989). Possibly the presence of mollusks on the upside and downside surfaces of the leaves represent a protective strategy against adverse climatic condition, predators, or simply a place for protected rest. In the present study, we observed a similar frequency of use of the upside and downside surfaces of leaves by some of the species observed, but in species such as *Chondropoma pictum* and *J. bicincta*, we observed differential use of only one side of the leaf. In *C. pictum* the upside was used with greater frequency, while, *J. bicincta* used the back in greater frequency.

Perhaps the variations of humidity between low and high strata are the causes of the distribution of the land snails in the vegetation, because the majority of individuals occurred in the first two strata. This result could be influenced by the abundance of operculated gastropods (*Chondropoma pictum*, *C. auberianum*, *Helicina aspersa*, *Alcadia hispida*, and *Torrella inmersa*), which are very susceptible to changes in relative humidity (Russell Hunter, 1964). As a survival strategy, these species frequent the lowermost zones of the vegetation near the litter, where humidity is conserved. It is possible that pulmonate species such as *Jeanneretia bicincta* and *Zachrysia auricoma* do not display similar strategies (to the operculated gastropods), but they frequented low shrubs. The presence of sources of foods (lichens and mosses) in branches-trunks may have conditioned a greater percentage of individuals to these substrates in contrast to the leaves, or perhaps branches-leaves are used as refuges. This research show that not all the species in the assembly of land snails studied present similar strategies of survival, where the micro-environmental conditions, physiological constraints, and distribution of the food items influence their occurrence. These studies are not totally conclusive because other parameters such as inter-specific competition may also play a role in patterning the distribution of species along the distinct vertical strata.

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LITERATURE CITED

Álvarez, J. and M.R. Willig. 1993. Effects of Treefall Gaps on the Density of Land Snails in the Luquillo Experimental Forest of Puerto Rico. Biotropica 25: 100–110.

Álvarez, J. and V. Berovides. 1989. Ecología y polimorfismo en *Liguus fasciatus* (Mollusca: Pulmonata) de Cayo Romano. Revista Biología 3: 183–196.

Bidart, L. and J. Espinosa. 1989. Aspectos del nicho ecológico de *Polymita picta nigrolimbata*, *Caracolus sagemon rostrata* y *Coryda alauda strobilus*. Ciencias Biológicas 21–22: 130–136.

Bidart, L., M. Osorio, E. Reynaldo, J. Fernández, and C. Iglesias. 1992. Nicho ecológico de *Polymita muscarum*, *Liguus fasciatus achatinus* y *Hermitrochus lucipeta*. Ciencias Biológicas 25: 9–19.

Cameron R.A.D. and B.M. Pokryszko. 2007. Forest snail faunas in the Kaszuby Uplands (Pomerania): a rich northern refuge. Folia Malacologia 14: 75–82.

Cañas, P. and S. Ysalgué. 1978. Mapas de naturaleza y recursos: Geomorfología. In: C.M. Ibarra et al. (eds.) Atlas de Cuba. La Habana, Cuba, pp. 30–31.

Čejka, T. and L. Hamerlik. 2009. Land snails as indicators of soil humidity in Danubian woodland (SW Slovakia). Polish Journal Ecology 57: 741–747.

Cook, A. 2001. Behavioural Ecology: On doing the right thing, in the right place at the right time. In: G.M. Barker (ed.) The biology of terrestrial molluscs, CAB International, Wallingford, pp. 447–487.

Correa-Sandoval, A., N.E. Strenth, R. Rodríguez, and J.V. Horta. 2009. Análisis ecológico básico de los gastrópodos terrestres de la Región Oriental de San Luis Potosí, México. Acta Zoologica Mexicana. (n. s.) 25: 105–122.

Cowie, R. 1985. Microhabitat choice and high temperature tolerance in the land snail *Theba pisana* (Mollusca: Gastropoda). Journal of Zoology 207: 201–211.

Espinosa, J. and J. Ortega. 2009. Moluscos Terrestres de Cuba. UCP Print, Vaasa, Finland, 191 pp.

Fernández, A. 2005. Plant species and strata selected by *Liguus fasciatus achatinus* Clench, 1934 (Mollusca: Orthalicidae) in semideciduous forest in El Yayal, Holguín Povince, Cuba. Of Sea and Shore 27: 89–92.

Fernández, A., J.A. La' O, C.R. Peña, P.G. González, and S.T. Monteagudo. 2000. Ecological niche of *Polymita muscarum* (Lea) and other land snails in the Pesquero Nuevo Beach's Lagoon, Rafael Freyre, Holguin, Cuba. Of Sea and Shore 23: 125–130.

Hermida, J., M.P. Ondina, and T. Rodriguez. 2000. The relative importance of edaphic factors on the distribution of some terrestrial gastropod species: Autecological and synecological approaches. Acta Zoologica Academiae Scientiarum Hungaricae 46: 265–274.

Hernández, M.H. 2011. Composición, estructura y uso de sustratos en las comunidades de moluscos terrestres del complejo de vegetación de mogote de Escaleras de Jaruco, Cuba. MS. dissertation. Universidad de la Habana, La Habana, 73 pp.

Jaremovic, R. and C.D. Rollo. 1979. Tree climbing by the snail *Cepaea nemoralis* (L.): a possible method for regulating temperature and hydration. Canadian Journal of Zoology 57: 1010–1014.

Kappes, H. 2005. Influence of coarse woody debris on the gastropod community (Mollusca: Gastropoda) in a managed calcareous beech forest in Western Europe. Journal of Molluscan Studies 71: 85–91.

Kappes, H., M. Jabin, J. Kulfan, P. Zach, and W. Topp. 2009. Spatial patterns of litter-dwelling taxa in relation to the amounts of coarse woody debris in European temperate deciduous forests. Forest Ecology and Management 257: 1255–1260.

Kappes, H., W. Topp, P. Zach, and J. Kulfan. 2006. Coarse woody debris, soil properties, and snails (Mollusca: Gastropoda) in European primeval forests of different climates. European Journal of Soil Biology 42: 139–146.

Kozlowski, J. and T. Kałuski. 2004. Preferences of *Deroceras reticulatum* (O.F. Muller), *Arion lucitanicus* Mabille and *Arion rufus* (Linnaeus) for various weed and herb species and winter oil seed rape (H group plants). Folia Malacologia 12: 173–180.

Luchtel, D.L. and I. Deyrup-Olsen. 2001. Body wall: form and function. In: G.M Barker (ed.) The biology of terrestrial molluscs, CAB International, Wallingford (U.K.), pp. 147–178.

Müller, J., C. Stratz, and T. Hothorn. 2005. Habitat factors for land snails in European beech forests with a special focus on coarse woody debris. European Journal of Forest Research 124: 233–242.

Nekola, J.C. 2009. Acidophilic terrestrial gastropod communities of North America. Journal of Molluscan Studies 76: 144–156.

Nekola, J.C. 2002. Effects of fire management on the richness and abundance of central North American grassland land snail faunas. Animal Biodiversity and Conservation 25: 53–66.

Perea J., A. Garcia, G. Gomez, R. Acero, F. Pena, and S. Gómez. 2007. Effect of light and substratum structural complexity on microhabitat selection by the snail *Helix aspersa* Muller. Journal of Molluscan Studies 73: 39–43.

Pérez, B. 1999. Composición y estructura ecológica de las malacocenosis en tres áreas cársicas de Sancti Spíritus. MS. Dissertation, Ciudad de la Habana, Cuba. 51 p.

Perrott, J. K., I.I. Levin, and E.A. Hyde. 2007. Morphology, distribution and desiccation in the brown garden snail (*Cantareus aspersus*) in northern New Zealand. New Zealand Journal of Ecology 31: 60–67.

Purchon, R.D. 1977. The Biology of the Mollusca. Pergamon Press, Inc., New York, 560 pp.

Russell-Hunter, W. 1964. Physiological aspects of ecology in nonmarine mollusks. In: K. M. Wilbur y C.M. Yonge (eds.) Physiology of mollusca, Vol. 1. Academic Press, New York, pp. 59–82.

Russell-Hunter, W. 1983. Overview: planetary distribution of and the ecological constraints upon the Mollusca. In: W.D. Russell-Hunter (ed.) The Mollusca, Vol. 6, Ecology, Academic Press, Orlando, Florida, pp. 1–27.

Santos, W.C. 2000. Algunos aspectos del nicho ecológico de *Polymita venusta* y *Hemitrochus* sp (Molusca Pulmonata), en la rocalla del Jardín Botánico "Cupaynicu". Revista Granma Ciencia 4: 1–7.

Schilthuizen, M. 2011. Community ecology of tropical forest snails: 30 years after Solem. Contributions to Zoology 80:1–15.

Sólymos, P., I. Czentye, and B. Tutkovics. 2006. Microscale distributions of landsnails in a homogenous alder stand. Soociana 34–35: 39–43.

Sólymos, P., R. Farkas, Z. Kemencei, B. Páll-Gergely, F. Vilisics, A. Nagy, M. Kisfali, and E. Hornung. 2009. Micro-habitat scale survey of land snails in dolines of the Alsó-hegy, Aggtelek National Park, Hungary. Mollusca 27: 167–171.

Stanisic, J. 1997. The distribution and patterns of species diversity of land snail in eastern Australia. Memoirs of the Queensland Museum 36: 207–214.

Stanisic, J., R.A.D. Cameron, B.M. Pokryszko, and J.C. Nekola. 2007. Forest snail faunas from S.E. Queensland and N.E. New South Wales (Australia): patterns of local and regional richness and differentiaton. Malacologia 9: 445–462.

Szybiak, K., J. Błoszyk, E. Koralewska-Batura, and B. Goldyn. 2009. Small-scale distribution of wintering terrestrial snails in forest site: relation to habitat conditions. Polish Journal Ecology 57: 525–535

First occurrence of putative hybridization in the genus *Lobatus* (Caenogastropoda: Strombidae)

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ABSTRACT

A putative hybrid *Lobatus gigas* × *L. gallus* is reported. It is compared with its putative parental species.

Additional Keyword: Caribbean

INTRODUCTION

Kronenberg (2008: 332, table) presented a review of known putative hybrids within the gastropod family Strombidae. A total of sixteen different combinations of putative parental species, all of Indo-Pacific origin, were indicated. Some of these were known from only one specimen, but others from over 100 specimens. Presumed cases of hybridization of Strombidae within the Caribbean are anecdotal, see for instance Conch-L archives (www.listserv.uga.edu), and restricted to *Strombus pugilis* Linnaeus, 1758 × *S. alatus* Gmelin, 1791. Images of such putative hybrids are published on the website of Bill Frank (www.jaxshells.org/strombss1ax.htm).

Reed (1995a, b) observed frequent interspecific mating between co-occurring species of Caribbean Strombidae with a remarkably little discrimination in choice of partner, i.e., males have frequently been observed attempting to mate with non-conspecific females. However, only matings of *S. pugilis* × *S. alatus* produced fertile eggs.

In May 2012 I received an e-mail from Harry G. Lee, from Jacksonville, Florida, who drew my attention to a putative hybrid *Lobatus gallus* (Linnaeus, 1758) × *L. gigas* (Linnaeus, 1758) in the private collection of Pete Stimpson, in Loudon, Tennessee. Subsequently, Dr. Stimpson made the specimen available for examination. The results are presented herein.

SYSTEMATICS

Family Strombidae Rafinesque, 1815

Genus *Lobatus* Swainson, 1837

Type Species: *Strombus bituberculatus* Lamarck, 1822 (= *Strombus raninus* Gmelin, 1791) by monotypy. Pliocene to Recent, Caribbean.

Discussion: The genus name *Lobatus* first appeared in 1837 in an anonymously compiled catalogue. Iredale (1921: 208) concluded that authorship of that catalogue should be attributed to Swainson. Therefore all newly introduced names in this catalogue should be attributed to Swainson. In his broad concept of the large, broad-winged Strombidae, Abbott (1960) synonymized *Lobatus* with *Tricornis* Jousseaume, 1886 (Type species: *Tricornis tricornis* (= *Strombus tricornis* [Lightfoot], 1786) by monotypy). Jung and Heitz (2001) argued that the introduction of *Lobatus* should be considered as a historical accident and considered the name unavailable.

The name *Lobatus* was further discussed by Kronenberg and Lee (2007) and Landau et al. (2008), who concluded that *Lobatus* was the first available name for the group of large, broad winged Strombidae from the Caribbean and Panamic Fauna province, rejecting the conclusions reached by Jung and Heitz (2001). Based on molecular (Latiolais et al., 2006) and morphological (Kronenberg, 2008) data it was concluded that *Lobatus* could not be considered a junior synonym of *Tricornis*.

***Lobatus gallus* (Linnaeus, 1758) × *Lobatus gigas* (Linnaeus, 1758)**
(Figures 1–5)

Description: Shell large, length from apex to tip of anterior canal 131 mm, consisting of about 9 teleoconch whorls and broad flaring outer lip (wing) with tip reaching beyond apex. Protoconch broken off and first teleoconch whorls badly eroded; of preserved teleoconch whorls second with axial costae, irregularly interrupted by broader costae, about three per whorl, here interpreted as varices. Costae gradually changing into pointed knobs on shoulder with abapical part of base adjacent to suture. Some knobs distinctly broader as a

Figures 1–5. Putative hybrid *Lobatus gallus* × *L. gigas*. Puerto Rico, off Mayagüez at about 4.6 m, September 1972, Pete Stimpson collection, unnumbered, height from apex to tip af anterior canal: 131 mm. **1.** Apertural view. **2.** Dorsal view. **3.** Lateral view, note relatively large shoulder knob. **4.** Apical view, same scale as Figures 1–3. **5.** Operculum, 40 mm length.

continuation of pattern of varices, last varical knob on antepenultimate whorl. Knobs gradually increasing in number and size, penultimate whorl with eleven knobs. On last whorl, knobs increasing in size at faster rate, penultimate knob largest, slightly past mid dorsum, last knob much smaller. Spiral sculpture much less prominent, on first teleoconch whorls eroded, on other spire whorls about seven discernible. Last whorl with prominent spiral cords abapically to shoulder knobs. Outer lip widely dilated, with adapical broadly rounded point, rim of lip slightly sinuous sloping down to point of attachment with ventral side of last whorl. Lateral part of outer lip slightly undulating on abapical half, corresponding with spiral cords on dorsal side, stromboid notch well developed. Adapertural side of outer lip smooth, columella smooth, apart from two narrow, low folds running into aperture. Anterior canal slightly developed. Callus on ventral side extended, thin, translucent, with gray-metallic haze on central part. Color of shell cream with irregular mottling of brown, rim of adapertural side of outer lip cream, aperture light pink; base of columella cream, adapical part light pink. Operculum stromboid, smooth edged, 40 mm in length. Soft parts unknown.

Material Examined: One specimen from Puerto Rico, west coast, off Mayagüez at about 4.6 m, September 1972, Pete Stimpson collection, unnumbered.

Distribution: So far only one specimen known, for data see above.

Remarks: In general the specimen is closest to *L. gallus*, both in general shape as well as size. Although usually smaller, the largest *L. gallus* measured attained a size of 134 mm from apex to tip of anterior canal. The hybrid specimen differs from *L. gallus* by its shorter anterior canal; the relative larger size of the penultimate shoulder knob on the last whorl; the shape of the posterior lobe of the outer lip, which is much more narrow in *L. gallus*; and the color of the aperture. In *L. gallus* the rim of the adapertural side of the outer lip and the columella are cream to pinkish light orange colored, but deep within the aperture it is always white. In the specimen here discussed, the rim of the outer lip is white, but deep within the aperture as well as the columella, it is pink, a color never seen in *L. gallus*.

Lobatus gigas grows to a much larger size, although dwarfs of about 150 mm are known. The hybrid specimen differs from *L. gigas* by its smaller size; slightly longer anterior canal, the shape of the posterior lobe of the outer lip; and the much larger knobs on the penultimate whorl.

DISCUSSION

The occurrence of the traits in the specimen reported herein could also be explained by developmental mutations within a specimen of one the putative parental species. However, in such a case one might expect that not so many shifts in shell characters reported herein as compared to one of the supposed parental species would occur, or one might expect one or more unique traits, i.e. shell characters that cannot be attributed to a character of one of the parental species or being intermediate between the supposed parental species. As this is not the case, and the specimen exhibits characters that are more or less intermediate between *L. gallus* and *L. gigas*, sometimes closer to either of these supposed parental species, I conclude that at present we are dealing with a putative hybrid *L. gallus* × *L. gigas*.

Several cases of putative hybridization within the Strombidae were summarized by Kronenberg (2008). All of these have been solely based on shell morphology and this case is no exception. The remarks by Kronenberg (1993), i.e., that the anatomy of the presumed hybrid was never examined nor that mating between supposed parental species was ever observed, are in fact still valid for all cases of presumed hybridization within Strombidae. Exceptional are observations made by Reed (1995a, b), who observed reproductive behavior of several species currently assigned to *Lobatus*, viz. *L. gigas*; *L. gallus*; *L. costatus* (Gmelin, 1791) and *L. raninus* (Gmelin, 1791). She observed mating between several species of *Lobatus* both in the field and in the laboratory. Apart from the observation that males occasionally attempted copulation with a male that already was engaged in copulation with a female, mating with non conspecific females was also observed. Reed (1995a) reported the following combinations: *L. gallus* ♂ × *L. costatus* ♀; *L. raninus* ♂ × *L. costatus* ♀; *L. raninus* ♂ × *L. gallus* ♀; and *L. gallus* ♂ × *L. raninus* ♀. Reed (1995b) also observed one case of multiple partners, i.e. copulation of *L. costatus* ♀ with *L. gallus* ♂ and *L. raninus* ♂. None of the females spawned after these copulations. Although *L. gigas* was present during these experiments, no mating between *L. gigas* and *L. gallus* or any other species of *Lobatus*, was reported.

It should be noted that "In a separate collection of *Strombus pugilis* and *S. alatus* individuals mated at random with no apparent distinction between species, and females spawned fertile egg masses, regardless of the male involved." (Reed, 1995a: 329). However, we don't know anything about further results, i.e., whether the eggs hatched or not. Within the genus *Lobatus*, *L. gallus* and *L. gigas* appear to be the most closely related species according to the cladogram presented by Latiolais et al. (2006). These authors did not incorporate *L. goliath* (Schröter, 1805) in their analysis. In an analysis based on anatomy (Simone, 2005), *L. gigas* and *L. goliath* group as sister taxa, which in turn are sister taxa to *L. costatus* and *L. gallus*.

Recently, Oxenford (2011) described a small population of *L. goliath* off Barbados, reported from two localities on the western coast of that island. In Barbadian waters, several species of Strombidae were already reported, among them *L. gigas* (Oxenford, 2011). Oxenford already noted that, although it is quite unlikely that *L. goliath* would have a serious negative impact on the marine ecosystem, it would be desirable to monitor this / these population(s) to record any developments. Taking into consideration the relatively large number of putative cases of hybridization in Strombidae (Kronenberg, 2008), the close relationship between *L. goliath* and *L. gigas* (Simone, 2005), and the behavior of Strombidae as reported by Reed (1995a, b), we cannot exclude the possibility that hybridization will occur. Of course, these species should also occur syntopic, i.e. not only living in the same geographical range but also sharing the same habitat.

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LITERATURE CITED

Abbott, R.T. 1960. The genus *Strombus* in the Indo-Pacific. Indo-Pacific Mollusca 1(2): 33–146.

Conch-L [Archives]. www.listserv.uga.edu (last accessed: 23 July 2012)

Iredale, T. 1921. Molluscan nomenclatural problems and solutions. Proceedings of the Malacological Society of London 14: 198–208.

Frank, W. (webmaster) www.jaxshells.org/strombss1ax.htm (last accessed: 23 July 2012)

Jung, P. and A. Heitz. 2001. The subgenus *Lentigo* (Gastropoda: Strombidae) in tropical America, fossil and living. The Veliger 44: 20–53.

Kronenberg, G.C. 2008. An intergeneric hybrid (Gastropoda: Caenogastropoda: Strombidae) with remarks on the subdivision of Indo-Pacific *Tricornis*. Basteria 72: 331–343.

Kronenberg, G.C. and H.G. Lee. 2007. Genera of American strombid gastropods (Gastropoda: Strombidae) and remarks on their phylogeny. The Veliger 49: 256–264.

Landau, B.M., G.C. Kronenberg, and G. Herbert. 2008. A large new species of *Lobatus* (Gastropoda: Strombidae) from the Neogene of the Dominican Republic, with notes on the genus. The Veliger 50: 31–38.

Latiolais J. M., M.S. Taylor, K. Roy and M.E. Hellberg. 2006. A molecular phylogenetic analysis of strombid gastropod morphological diversity. Molecular Phylogenetics and Evolution 41: 436–444.

Oxenford, H.A. 2011. A giant leap? Goliath conch a Brazilian endemic species is found in Barbados. Journal of the Barbados Museum and Historical Society 57: 192–201.

Reed, S. E. 1995a. Reproductive anatomy and biology of the genus *Strombus* in the Caribbean: I. Males. Journal of Shellfish Research 14: 325–330.

Reed, S. E. 1995b. Reproductive anatomy and biology of the genus *Strombus* in the Caribbean: II. Females. Journal of Shellfish Research 14: 331–336.

Simone, L.R.L. 2005. Comparative morphological study of representatives of the three families of Stromboidea and the Xenophoroidea (Mollusca, Caenogastropoda), with an assessment of their phylogeny. Arquivos de Zoologia 37: 141–267.

[Swainson, W.] 1837. Catalogue of the Foreign Shells in the possession of the Manchester Natural History Society, arranged according to the system of Lamarck. 99 pp. [not seen]

Research Note

New distribution record for the rare limpet *Acroloxus coloradensis* (Henderson, 1930) (Gastropoda: Acroloxidae) from Montana

The Rocky Mountain Capshell, *Acroloxus coloradensis* (Henderson, 1930), the only North American member of the basommatophoran family Acroloxidae, is broadly distributed across southern Canada and south into the Rocky Mountains in the USA (Turgeon et al., 1998; Lee and Ackerman, 2000). Despite its wide geographic range, *A. coloradensis* has been documented from < 30 locations, mostly in British Columbia, Alberta, Ontario, and Quebec (Lee and Ackerman, 2000; Anderson, 2005). Relict populations of *A. coloradensis* in the USA have been documented from only 6 sites in Colorado and 2 sites in Glacier National Park (Glacier NP), Montana (Anderson, 2005; Ellis et al., 2004). In Glacier NP, *A. coloradensis* was first reported from Lost Lake (Figure 1; Russell and Brunson, 1967). A second population in the park was discovered in Trout Lake in 2001 (Ellis et al., 2004). In both lakes, *A. coloradensis* was found primarily under rocks and other cover objects.

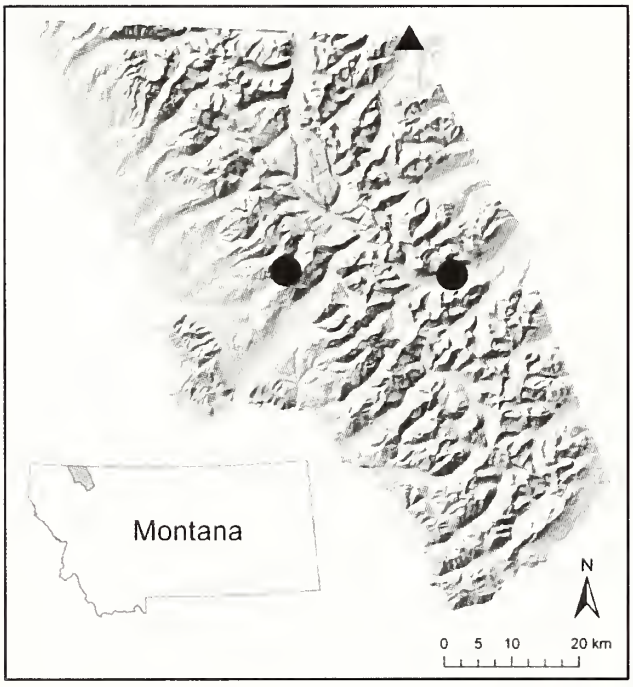

Figure 1. Documented locations of the Rocky Mountain Capshell (*Acroloxus coloradensis*) in Glacier National Park, Montana. The location of the newly discovered population is marked with a triangle. The Lost Lake and Trout Lake populations are marked with circles.

We report the incidental collection of a single *Acroloxis coloradensis* specimen (5mm total length) from a small, unnamed beaver-dammed lake (1.04 ha, 1391 m elevation; N 48.996°, W –13.678°) in the Belly River Valley in Glacier NP (Figures 1–2). The limpet was collected during a site survey for amphibians on 30 July 2012. The shallow margins of the lake are dominated by organic substrates that support extensive emergent vegetation. Electrical conductivity of the lake was 370 µS, which is high compared to other small lakes in Glacier NP (BRH, unpublished data). A secondary goal of these surveys was to collect ≤ 30 large gastropods that get captured while using dip-nets (4.75 mm mesh) to sample for amphibian larvae. The *A. coloradensis* specimen, characterized by its flat shell and apex that points to the rear and left, was found among several preserved *Planorbella trivolvis* and *Physella* sp. Because our survey protocol for amphibian larvae does not include turning cover objects and it is unlikely the limpet would have been picked from the bottom of a net, we suspect the *A. coloradensis* specimen was along with *Planorbella trivolvis* and *Physella* sp.

Acroloxus coloradensis is classified as vulnerable by the IUCN because of the small number of documented populations and their isolation from one another (Bogan, 1996). The rarity of this species makes the discovery of new populations important for accurate risk assessments.

Figure 2. Rocky Mountain Capshell (*Acroloxus coloradensis*) collected from the Belly River Valley, Glacier National Park, Montana. Total length of the specimen was approximately 5 mm.

Our record of *A. coloradensis* in the northeast corner of Glacier NP in a habitat that differs from the other 2 locations in the park suggests it may be more widely distributed in the area than records indicate. Additional work will be required to determine the relative abundance of *A. coloradensis* at this newly documented population and to determine if it is present in neighboring water bodies.

ACKNOWLEDGMENTS

We thank P. Scarr and S. Dykman for their careful field work and S. Schwartz for help with the photograph. R.T. Dillon (College of Charleston) confirmed identification of the specimen. Reviews by A.E. Bogan, B. Roth, and J. Giersch improved the manuscript. This work was funded by USGS Amphibian Research and Monitoring Initiative (ARMI) and was conducted under research permit GLAC-2011-SCI-0025. This note is ARMI product no.430.

LITERATURE CITED

Anderson, T. 2005. Rocky Mountain capshell snail (*Acroloxus coloradensis*): a technical conservation assessment. USDA Forest Service, Rocky Mountain Region. Available: *http://www.fs.fed.us/r2/projects/scp/assessments/rockymountaincapshellsnail.pdf*. (31 January 2013).

Bogan, A.E. 1996. *Acroloxus coloradensis*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. <*www.iucnredlist.org*>. (16 September 2012).

Ellis, B. K., L. Marnell, M. A. Anderson, J. A. Stanford, C. Albrecht and T. Wilke. 2004. Status and ecology of a glacial relict mollusk, the Rocky Mountain capshell limpet (*Acroloxus coloradensis*), in relation to the Limnology of Lost Lake, Glacier National Park, Montana (USA). Open File Report 186-05. Prepared for the National Park Service, Glacier National Park, West Glacier, Montana by Flathead Lake Biological Station, University of Montana. 63pp.

Henderson, J. 1930. *Ancylus coloradensis*, new name for *A. hendersoni* Walker, 1925, not 1908. The Nautilus 44: 31.

Lee, J. S., and J. D. Ackerman. 2000. Freshwater molluscs at risk in British Columbia: Three examples of "risk". Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, 2000, Kamloops, B.C., Volume One, B.C. Ministry of Environment, Lands and Parks, Victoria, B.C. and University of the Cariboo, Kamloops, B.C. 490pp.

Russell, R. H. and R. B. Brunson. 1967. *Acroloxus coloradensis* from Montana. The Nautilus 81: 33.

Turgeon, D.D., J.F. Quinn, Jr., A.E. Bogan, E.V. Coan, F.G. Hochberg, W.G. Lyons, P.M. Mikkelsen, R.J. Neves, C.F.E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F.G. Thompson, M. Vecchione, and J.D. Williams. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks, 2nd edition. American Fisheries Society, Special Publication 26, Bethesda, ix + 526 pp.

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Notice

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Antarctica, where turrids and whelks converge: A revision of *Falsimohnia* Powell, 1951 (Neogastropoda: Buccinoidea) and a description of a new genus

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ABSTRACT

A study of the type material of Antarctic species of conoideans described by Herman Strebel revealed that four species, all originally described in the genus *Bela* Gray, 1847 (Mangeliidae), are referable to the superfamily Buccinoidea based on radular morphology. Three of the species: *B. fluvicans*, *B. minor*, and *B. anderssoni* are transferred to the genus *Falsimohnia*, which is here reviewed. The new buccinoidean genus *Strebela* is proposed for the species originally described as *Bela notophila*. Of the five species of the conchologically similar genus *Pareuthria* Strebel, 1905 that have been recorded within the Antarctic Convergence, two, *Pareuthria innocens* (Smith, 1907) and *P. hoshiaii* Numanami, 1996, are transferred to the genus *Falsimohnia* based on radular morphology. The appropriate generic allocation of *Pareuthria plicata* Thiele, 1912 is not yet clear; however, major differences in radular morphology exclude it from the genus *Pareuthria*. The taxa *Pareuthria valdiviae* (Thiele, 1925) and *Pareuthria turriformis* Egorova, 1982 are presently known only from their shell morphology. We suggest that they will be referred to other genera when anatomical material becomes available, and that the genus *Pareuthria* will be limited to the Magellanic region.

Additional Keywords: Gastropoda, Conoidea, Buccinoidea, Antarctic Convergence, biogeography, morphological convergence

INTRODUCTION

Despite numerous and ongoing research programs that have been sampling areas of the Southern Ocean for more than a century, many of the species of Neogastropoda described from Antarctic waters are known from a small number of specimens, and a considerable proportion of the taxa have yet to be re-sampled since their original description. Therefore, it is not surprising that some of the smaller species, especially those having narrow distributions, remain poorly studied. Among the insufficiently studied groups within Antarctic waters are the Conoidea. This superfamily is one of the most diverse clades of Neogastropoda (Bouchet, et al., 2002; Bouchet, et al., 2009), particularly in the tropics. The classification of the superfamily Conoidea has recently been revised based on radular morphology (Tucker and Tenorio, 2009) and molecular phylogeny (Puillandre et al., 2011), and now includes 15 families (Bouchet et al., 2011). Thirteen of these families had previously been included in a single family, the Turridae, which emerged as paraphyletic in the phylogenetic analysis. These 13 families are collectively referred to here as "turrids". Currently, about 460 conoidean genera and subgenera are recognized, 358 of which belong to "turrid" families and encompass more than 4000 named Recent species (Tucker, 2004), with many hundreds of species still unnamed (Bouchet, et al., 2009).

The diversity of turrids decreases significantly in high latitudes. Only about 40 species are known to inhabit the waters of the Arctic Ocean (Kantor and Sysoev, 2006). The diversity of turrids in Antarctic and subAntarctic waters is also very low. At present, 37 named species have been recorded from the Southern Ocean (Engl, 2012), although there are still new species to be discovered and named. Remarkably, the number of presently recognized Arctic and Antarctic turrids is nearly the same.

The majority of the known Antarctic turrids were described in publications based on the large Antarctic expeditions of the early 20th Century (Strebel, 1908, Thiele, 1912, Hedley, 1916). Hermann Strebel (1908) described numerous gastropods using material collected by the Swedish Antarctic Expedition (1901–1903) under the command of Otto Nordenskjöld. Among these were 11 new species of turrids, of which ten were from within the Antarctic Convergence (Strebel, 1908:87), the highest number of species of Antarctic Conoidea to be described in a single publication. All of the species described by

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Strebel were considered valid by most subsequent authors (e.g., Powell, 1951, Engl, 2012). Five of Strebel's species are rather common in collections and are often referred to in the literature. Of these, four serve as type species of subsequently described genera:

- *Surcula magnifica* Strebel, 1908 (=*Aforia magnifica*, family Cochlespiridae Powell, 1942)
- *Bela antarctica* Strebel, 1908 (= *Conorbela antarctica*, type species of the genus *Conorbela* Powell, 1951, family Pseudomelatomidae Morrison, 1965)
- *Bela pelseneri* Strebel, 1908 (= *Propebela (Lorabela) pelseneri*, type species of the subgenus *Lorabela* Powell, 1951, family Mangeliidae P. Fischer, 1883)
- *Bela purissima* Strebel, 1908 (= *Typhlodaphne purissima*, type species of the genus *Typhlodaphne* Powell, 1951, family Borsoniidae A. Bellardi, 1875).
- *Bela turrita* Strebel, 1908 (=*Belaturricula turrita turrita*, type species of the genus *Belaturricula* Powell, 1951, family Borsoniidae)

The remaining five Antarctic species described by Strebel (1908) as turrids are less well known, and all but *Pleurotomella bathybia* are reviewed here. Thanks to the courtesy of Dr. Anders Warén we were able to study the type material of Strebel's species in the collections of the Swedish Museum of Natural History, Stockholm, including the radulae of three of the species.

The holotype of *Pleurotomella bathybia* had been lost some time ago, and a neotype (ZSM Mol 2002 1313) has only recently been designated (Engl, 2012: 185, pl. 76, fig. 2a) from off South Georgia, near the locality where Strebel's holotype was collected. As this taxon is presently known only from its shell and protoconch morphology, it is provisionally retained within Conoidea.

The radulae and shell characters of the four species treated herein (all originally described in the turrid genus *Bela*) clearly demonstrate that these taxa belong in the superfamily Buccinoidea. Radular morphology indicates a close affinity to the genus *Falsimohnia* Powell, 1951. In this paper we review the genus *Falsimohnia* and include a redescription of four of Strebel's species.

MATERIALS AND METHODS

The type specimens of species described by Strebel are housed in Swedish Museum of Natural History. We also examined specimens from the Muséum national d'Histoire naturelle, and the Institute Royal des Sciences Naturelles de Belgique for comparative purposes.

Radulae were cleaned with diluted bleach (1 part of commercially available bleach to 3–4 parts of distilled water), mounted on round glass cover slips and air-dried. Cover slips were then mounted onto SEM stubs, coated with gold and examined under a JEOL JSM 840A scanning electron microscope. Abbreviations used in text: AL: Aperture length; AW: Aperture width; IRSN: Institute Royal des Sciences Naturelles de Belgique, Brussels; MNHN: Muséum national d'Histoire naturelle, Paris; NHMUK: The Natural History Museum, London; SL: Shell length; SMNH: Swedish Museum of Natural History, Stockholm; ZMB: Zoological Museum of Berlin, Berlin; ZSM, Zoologische Staatssammlung München, Munich.

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Superfamily Buccinoidea Rafinesque, 1815
Family Buccinulidae Finlay, 1928
Subfamily Cominellinae Gray, 1857

Genus *Falsimohnia* Powell, 1951

Falsimohnia Powell, 1951: 137; Engl, 2012:145.

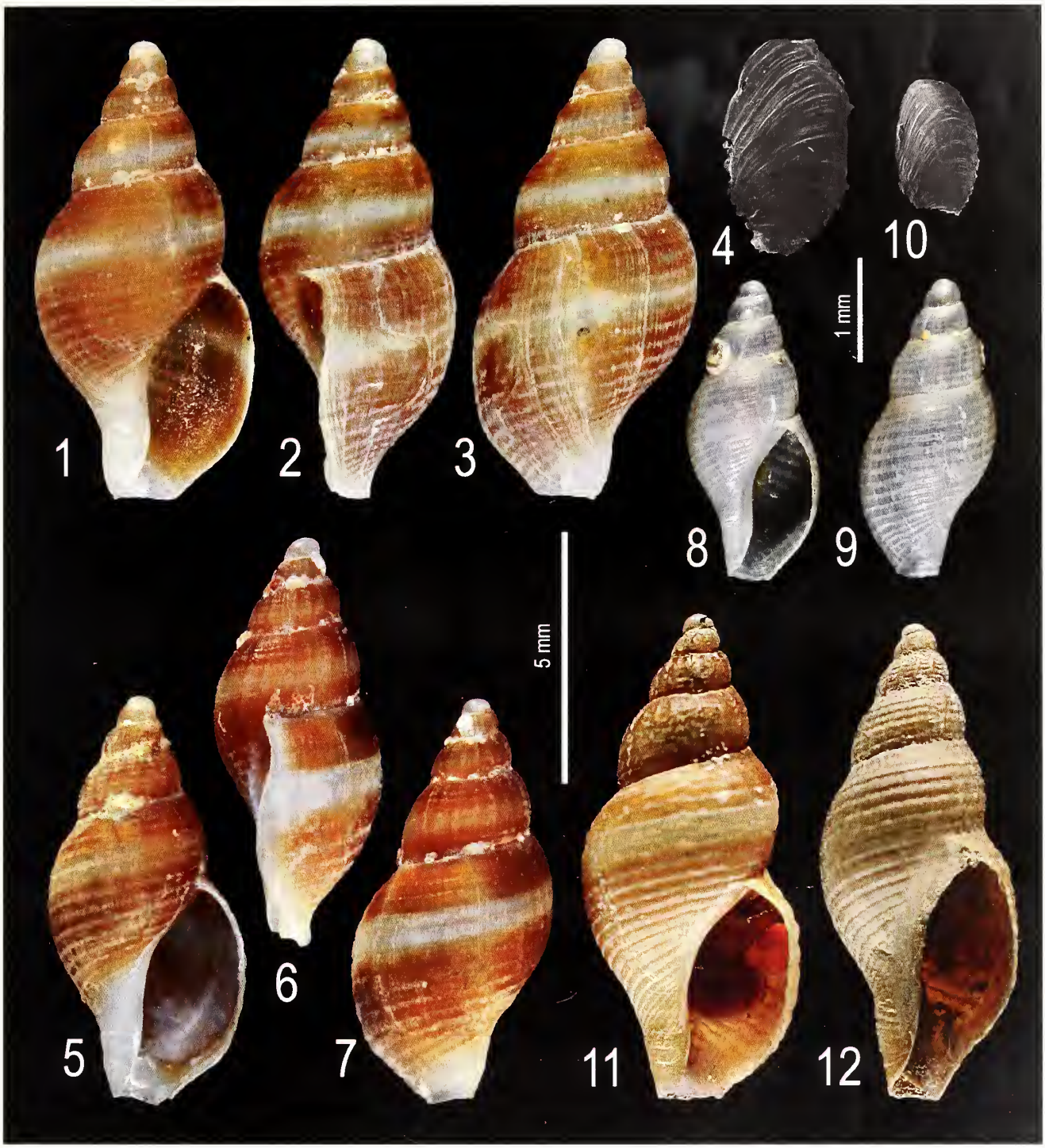
Type Species: *Buccinum albozonatum* Watson, 1882:358, by original designation.

Description: Shell small to medium-sized (to 12 mm), broadly fusiform, with high, convex last whorl and short to slightly attenuated canal. Protoconch paucispiral, smooth. Spiral sculpture usually of well-defined cords, covering entire shell surface. Axial sculpture of weakly pronounced, low, narrow, broadly spaced, and slightly sigmoidal axial ribs most prominent on spire whorls. Operculum oval, with terminal or subcentral nucleus, situated in the lower corner of operculum. Radula with rachidian teeth nearly as long as wide, V-shaped, with deep anterior notch and long, single, medial cusp emanating from posterior edge. Lateral teeth with long basal plate bearing two long, curved cusps near middle and inner margin of tooth. Outer portion of basal plate tapered, without cusps. Outer cusp broader, longer, inner cusp shorter, generally more curved.

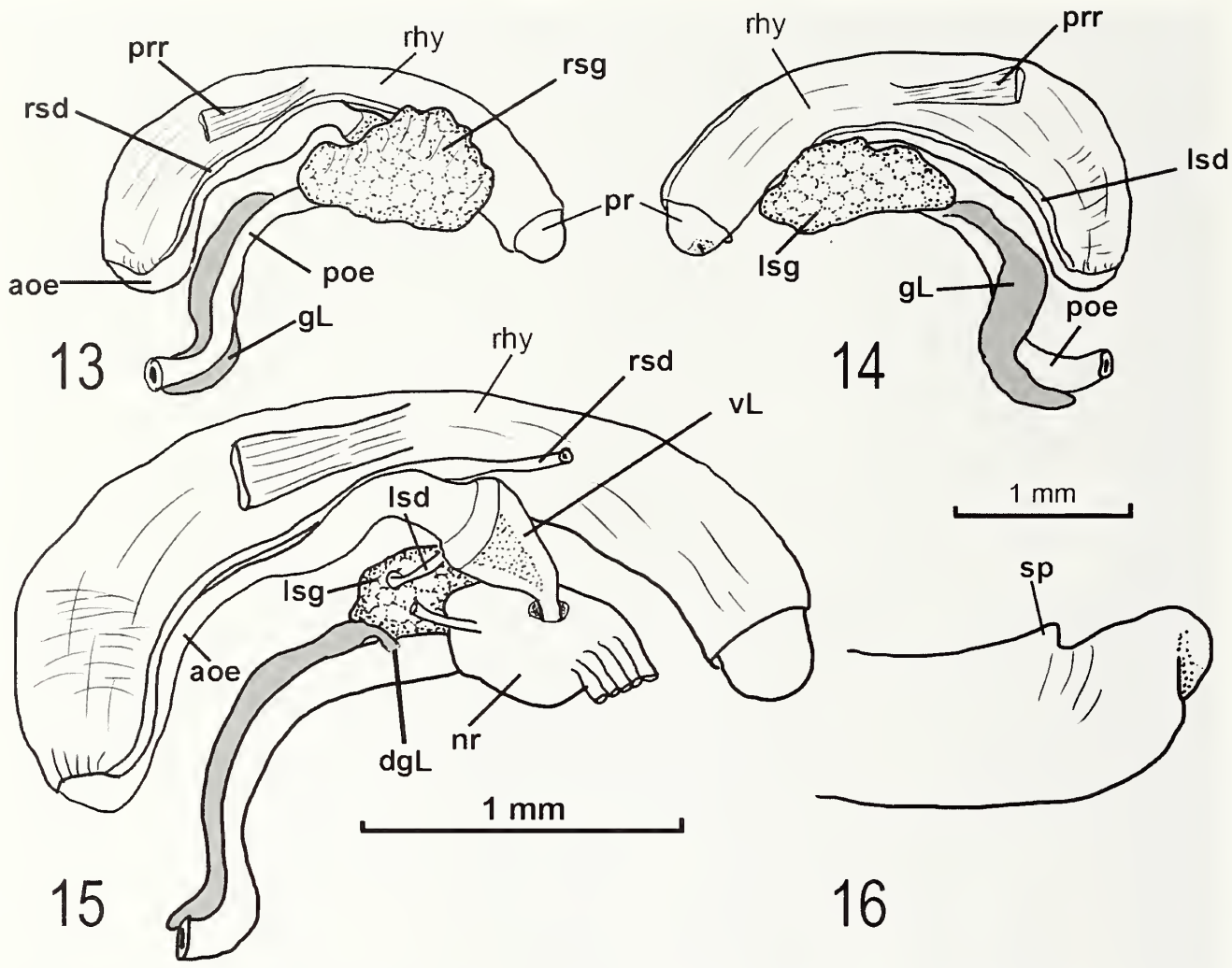
Remarks: Powell (1951: 137) based his monotypical genus *Falsimohnia* entirely on radular characters as a "derivative of *Pareuthria* in which the normal three cusps of the central tooth have been reduced to a single member", noting also the similarity in the opercula of the two genera. He designated *Buccinum albozonatum* Watson, 1882 from Kerguelen Island as the type species, and went on to diagnose this genus by emphasizing conchological similarities with the genera *Pareuthria* Strebel, 1905 and *Glypteuthria* Strebel, 1905, but explicitly differentiated *Falsimohnia* on the basis of its having a radula similar to that of the Arctic genus *Mohnia* Friele, 1878, in which the rachidian tooth has a single cusp and the lateral teeth are bicuspid. The description of *Falsimohnia* did not provide any additional conchological or anatomical diagnosis.

Falsimohnia albozonata (Watson, 1882)
(Figs 1–7, 13–19)

Buccinum albozonatum Watson, 1882: 358; Watson, 1886: 212, pl. 13, fig. 7.



Figures 1–12. Species of *Falsimolnia*. **1–7.** *Falsimolnia albozonata* (Watson, 1882). **1–3.** Shell, and **4.** operculum, MNHN uncataloged, Kerguelen Islands, Iles Nuageuses, R/V Marion Dufresne, cruise 04, st. CP17, 48°47,1′ S, 68°49.3′ E, 70 m, (SL = 9.2 mm). **5–7.** IRSN, IG 26482, Kerguelen Islands, S of Ile Suhin, 40 m, (SL = 8.2 mm). **8–10.** *Falsimolnia* cf. *albozonata*. **8–9.** Shell and **10.** operculum, MNHN uncataloged, Crozet Islands, R/V Marion Dufresne, cruise 03, st. CP17, 46°24′ S, 51°59′ E, 180 m, (SL = 6.0 mm). **11–12.** *Lachesis australis* Martens and Thiele, 1904. ZMB 59955, Syntypes. **11.** This syntype (ZMB 59955a) is designated as the lectotype of *Lachesis australis* Martens and Thiele, 1904, herein. **12.** This syntype (ZMB 59955b) becomes the paralectotype of *L. australis*. The 5 mm scale bar applies to all shells, the 1 mm scale bar applies to opercula.



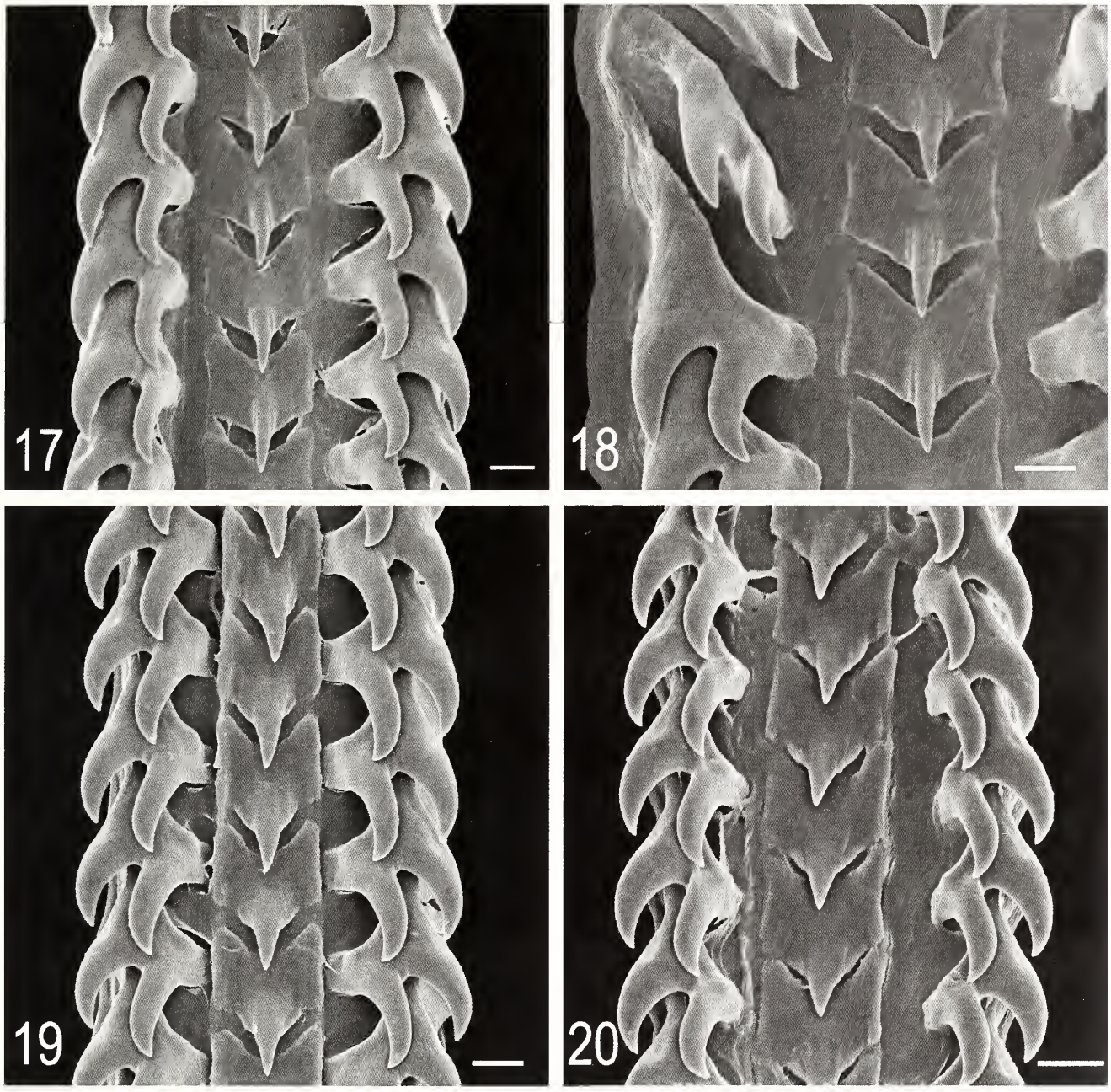
Figures 13–16. Anatomy of *Falsimohnia albozonata*. **13.** Right lateral and **14.** left lateral views of the anterior foregut. **15.** Right lateral view or anterior foregut with right salivary gland removed to show the duct of the gland of Leiblein and valve of Leiblein. **16.** Detail of distal end of penis. **aoe**, anterior oesophagus; **dgl**, duct of the gland of Leiblein; **gL**, gland of Leiblein; **lsd**, duct of the left salivary gland; **lsg**, left salivary gland; **nr**, circumoesophageal nerve ring; **poe**, posterior oesophagus; **pr**, proboscis; **prr**, proboscis retractors; **rhy**, rhynchodaeum; **rsd**, duct of the right salivary gland; **rsg**, right salivary gland; **sp**, seminal papilla; **vL**, valve of Leiblein.

Lachesis? *australis* Martens and Thiele, 1904: 62, pl. 5, fig. 18.
Pareuthria albozonata—Thiele, 1912: 244.
Falsimohnia albozonata—Powell, 1951: 138.
? *Mangelia nigropunctata* Martens, 1885: 91-92.
? *Mangelia antarctica* Martens and Pfeffer, 1886: pl. 1, figs. 5 a, b.

Type Localities: Royal Sound, Kerguelen Islands, 49°28′ S, 70°13′ E, 28 fms [51 m] (*B. albozonatum*); Kerguelen Islands (*L. australis*); South Georgia (*M. nigropunctata, M. antarctica*).

Material Examined:, IRSN IG 26482, Kerguelen Islands, S of Ile Suhin, 40 m, 3 live, 1 dissected (Figures 1 E–G); MNHN, uncataloged, Kerguelen Islands, Iles Nuageuses, R/V Marion Dufresne, cruise 04, st. CP17, 48°47.1′ S, 68°49.3′ E, 70 m (Figures 1 A–D); MNHN, uncataloged, Crozet Islands, R/V Marion Dufresne, cruise 30, st. DC60, 46°25′ S, 50°22′ E, 105-120 m (11 dead); MNHN, uncataloged, Crozet Islands, R/V Marion Dufresne, cruise 03, st. CP17, 46°24′ S, 51°59′ E, 180 m (1 live, radula examined, light form) (Figures 8–10).

Description: Shell medium-sized (to 10 mm), strong, broadly fusiform, with evenly convex whorls and short, broad siphonal canal. Protoconch rounded, smooth, paucispiral. Axial sculpture limited to growth lines, occasionally with narrow, broadly spaced, low, slightly prosocline ribs more pronounced on upper teleoconch whorls. Spiral sculpture of low rounded cords (9–11 on penultimate whorl, 16–19 on last whorl) slightly



Figures 17–20. *Falsimohnia albozonata* radulae. **17–18.** Radula of specimen in figures 1–3, MNHN uncataloged, Kerguelen Islands, Iles Nuageuses, *Marion Dufresney*, cruise 04, st. CP17, 48°47,1′ S, 68°49.3′ E, 70 m. **19.** Radula of specimen in figures 5–7, IRSN, IG 26482, Kerguelen Islands, S of Ile Suhin, 40 m. **20.** *Falsimohnia* cf *albozonata*. Radula of specimen in figures 8–9, MNHN uncataloged, Crozet Islands, R/V Marion Dufresne, cruise 03, st. CP17, 46°24′ S, 51°59′ E, 180 m. Scale bars = 10 µm.

narrower that the interstices. Aperture elongated (AL/SL ≈ 0.55–0.57), narrow (AL/AW ≈ 2.2), elliptical, with narrow callus extending onto parietal and columellar regions of inner lip. Operculum oval, with terminal nucleus. Periostracum thin, tightly adherent, transparent. Shell light brown to rust-colored, with a characteristic whitish spiral band along shell periphery, whitish columella and siphonal canal.

Gross Anatomy: Last whorl of the animal of a single specimen (IRSN IG 26482, SL 8.2 mm) was extracted from the shell and dissected. Preserved tissues lack pigmentation. Foot short, truncated posteriorly, operculum missing, likely lost during fixation (opercular disk distinct). Mantle cavity deep (L/W ≈ 2), mantle edge did not cover head. Siphon short, very broad. Head small, with long, closely spaced tentacles, large, brown eyes on

very small lobes at tentacle bases. Disposition of mantle cavity organs typical for Buccinoidea. Ctenidium narrow, spanning ¾ of mantle cavity, osphradium equal in width to ctenidium, slightly shorter. Hypobranchial gland without distinct folds. Rectum very short, broad. Proboscis (Figure 14, pr) long, narrow, about 3.2 mm in length (0.7 AL). Proboscis retractor muscles (Figures 13, 14, prr) very thin, paired, symmetrical, attached to rhynchodaeum (Figures 13–15, rhy) at mid-length. Salivary glands (Figures 13, rsg, 14, 15, lsg) medium-sized, oval, fused ventral to rhynchodaeum, covering nerve ring (Figure 15, nr) and most of valve of Leiblein (Figure 15, vL). Salivary ducts (Figures 13, rsd, 14,15, lsd) very thick, running along both sides of anterior oesophagus. Valve of Leiblein well defined, conical. Gland of Leiblein (Figures 13, 14, gL) small, simple, tubular, colorless, joins esophagus through a slightly constricted duct posterior to nerve ring. Odontophore spans ⅔ of proboscis length. Subradular cartillages fused along entire length. Radula equal to odontophore in length. Radula (Figures 17–19) narrow, about 75–90 µm wide (1.6–1.8% of AL). Lateral teeth with long base tapered toward the outer edge, with two strong, curved cusps, the inner cusp slightly shorter, emanating from the inner half of the tooth. Rachidian tooth with a V-shaped base nearly as long as wide, deeply notched anteriorly and with one strong, long cusp emanating from posterior midline of the tooth.

Remarks: We did not examine the holotype of *Buccinum albozonatum*, but studied several specimens collected close to the type locality (Kerguelen). Conchologically they are very similar to the published description (Watson, 1882) and subsequent illustrations (Watson, 1886:pl. 13, fig. 7) of this species. We do note, however, that all specimens we examined had a slightly different operculum. Watson (1886) stated that "Operculum is intermediate in form between that of *Buccinum* and *Cominella*; for, as in the latter, the nucleus is at the lower end, but it is not apical, but is within the edge towards the outer margin as in the former." In the specimens we studied, most opercula are eroded to varying degrees (Figure 4), yet their general shape indicates that their nuclei are terminal, not subcentral. In other respects the shells of the specimens examined are very similar to the figure published by Watson. The opercula of the samples we examined matched the illustration of the operculum of *F. albozonatum* that was published by Powell (1951: fig. N, 127).

Powell (1951:138) considered *Falsimohnia albozonata* to have a broad geographic range, and synonymized *Mangelia antarctica* Martens and Pfeffer, 1886 (from South Georgia Island) and *Lachesis? australis* Martens and Thiele, 1903 (from Kerguelen Island). The name *Mangelia antarctica* was unnecessary replacement name for *Mangelia nigropunctata* Martens, 1885 from South Georgia (Zelaya, 2005).

We were not able to examine the type material of *Mangelia nigropunctata*. However, Martens and Pfeffer's illustrations (1886:pl. 1, fig. 5) indicate that their taxon is very similar to *F. albozonata*, and also has the whitish spiral band along the shell periphery that is present in *F. albozonata*. As we have not found any material of *F. albozonata* from South Georgia, we cannot confirm the presence of this taxon off South Georgia, nor its status as senior synonym of *M. nigropunctata* (= *M. antarctica*).

Powell (1951: fig. K, 59) illustrated the radular dentition of a specimen collected off South Georgia Island that he attributed to *F. albozonata*. A reexamination of voucher material (station 149) identified by Powell and deposited in the Natural History Museum (NHMUK 1961499) revealed the specimens to be referable to *F. fulvicans* (see below for further discussion).

Another species that Powell (1951) considered to be a synonym of *F. albozonata* is *Lachesis australis*, also from Kerguelen. Two syntypes of *L. australis* were located in the Zoological Museum of Berlin (ZMB 59955) (Figures 11–12). One of the specimens (Figure 11) matches typical *Falsimohnia albozonata*, while the other (Figure 12) differs in having a more slender shell with a more elongated aperture and uniform coloration, lacking the whitish band along the shell periphery and siphonal canal. We examined a similar specimen from Crozet Islands (Figures 8–10) and found the radula (Figure 20) to be identical to that of typical specimens of *F. albozonata* (Figures 17–19). It is at present unclear whether the conchological differences are due to intraspecific variation, or whether the two morphotypes represent different species of *Falsimohnia*. In order to stabilize the nomenclature, we here designate the specimen illustrated in Figure 11 (ZMB 59955a) as lectotype of *Lachesis australis* Martens and Thiele, 1904. The remaining specimen (Figure 12, ZMB 59955b) becomes a paralectotype. As the lectotype has all the morphological features of *Falsimohnia albozonata*, *Lachesis australis* Martens and Thiele, 1904, is a junior subjective synonym of *Buccinum albozonatum* Watson, 1882.

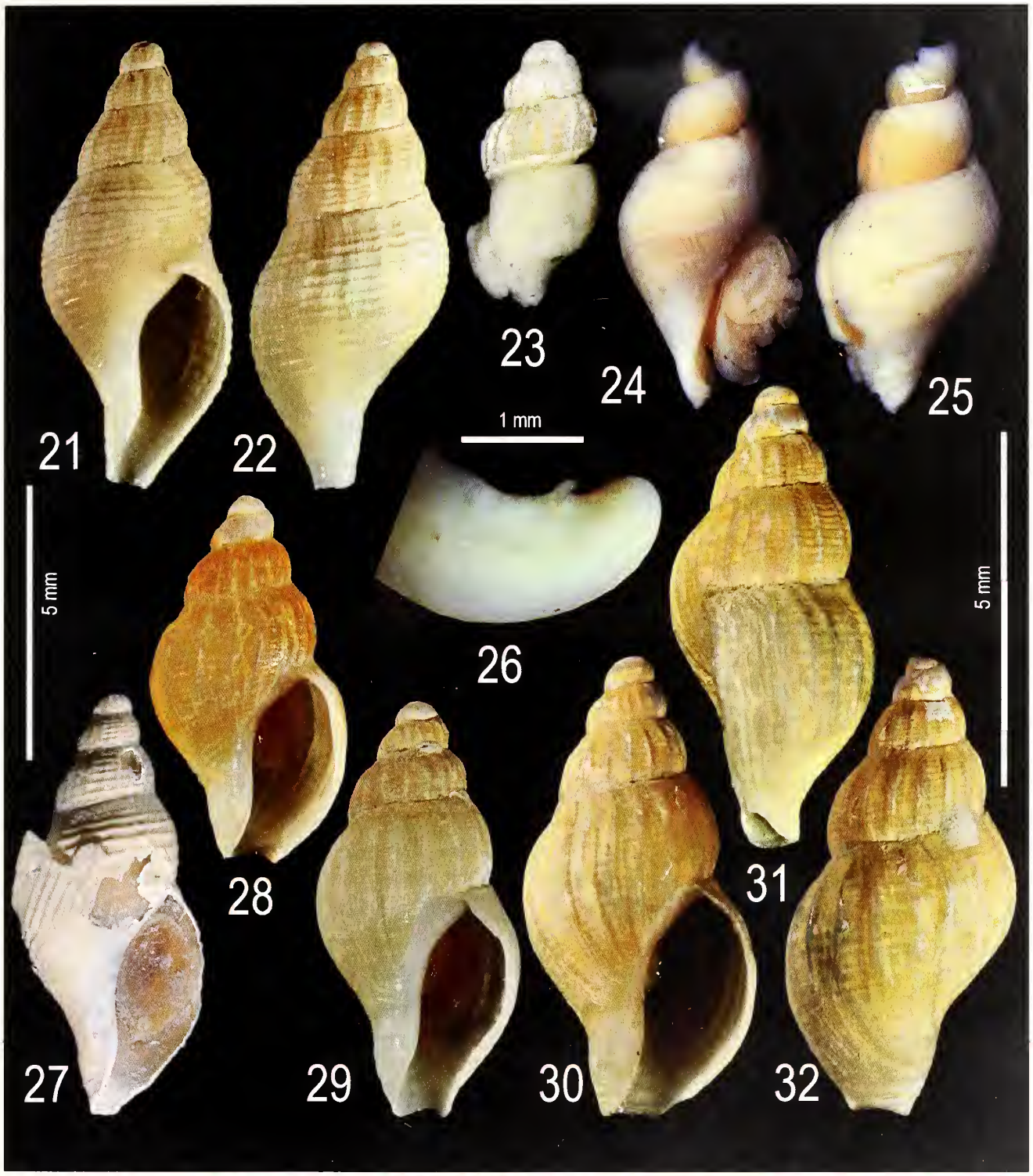
Falsimohnia fulvicans (Strebel, 1908)

(Figures 21–27, 35–36)

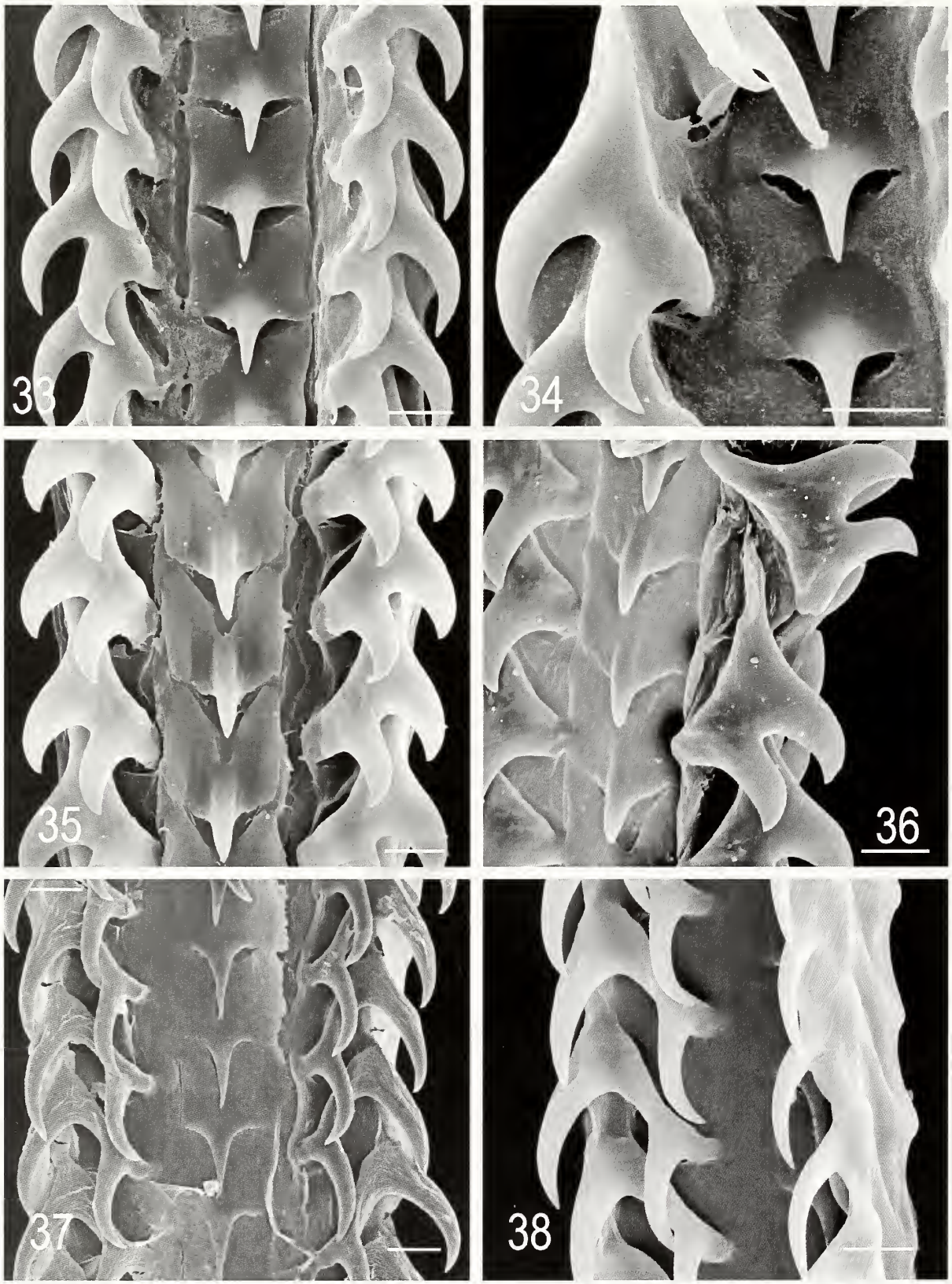
Bela fulvicans Strebel, 1908: 15, Taf. 2, fig. 25 a–d; Melvill and Standen, 1912: 356; Powell, 1951: 56 (Burwood Bank), 59 (South Georgia); Zelaya, 2005: 128, fig. 52 (figure erroneously labelled as *Lorabela pelseneeri*); Engl, 2012: 181, pl. 73, fig. 7a–c.

Type Locality: South Georgia, Cumberland Bay, outside Grytviken, 54°22′ S, 36°27′ W, 24–52 m (Swedish South Polar Expedition, sta. 25). [The coordinates provided on the printed label accompanying the specimen and in Strebel's original description are likely erroneous, as they correspond to a location on dry land close to Grytviken.]

Type Material: Lectotype, SMNH Type 6303 (designated by Engl, 2012: p. 181) (Figures 21–22). Paralectotypes: SMNH Type 1030 (st. 34, Cumberland Bay, 54°11′ S, 36°18′ W, 252–310 m) (Figures 24–26);



Figures 21–32. Species of *Falsimohnia*. **21–27.** *Falsimohnia fulvicans* (Strebel, 1908). **21–22.** Lectotype, (SMNH Type-6303), (SL 8.1 mm). **23.** Paralectotype, (SMNH Type-6159). **24–25.** Body of paralectotype (SMNH Type 1030) **26.** penis tip of paralectotype in figures 24–25. **27.** Specimen from South Georgia identified by Powell as *Falsimohnia albozonata*, NHMUK 1961499, (SL 7.6 mm). **Figures 28–32.** *Falsimohnia minor* (Strebel, 1908). Syntypes (SMNH Type-1057). **28.** (SL 5.6 mm). **29.** (SL 5.8 mm). **30–32.** (SL 6.5 mm). Left scale bar applies to figures 21,22, 27, right scale bar applies to figures 28–32. The 1mm scale bar applies to figure 26.



Figures 33–38. Radulae. **33–34.** *Falsimohnia minor* (Strebel, 1908), radula from syntype in figure 29. **35–36.** *F. fulvicans* (Strebel, 1908), radula from paralectotype in figures 24–25. (SMNH Type 1030). **37–38.** *Strebelona notophila* (Strebel, 1908), radula from holotype, Figures 44–45 (SMNH Type-1064). Scale Bars = 10 μm.

SMNH Type 6159 (st. 95, off Astrolabe Island, 64°09′ S, 58°17′ W, 95 m) (Figure 23).

Description (based on intact shell of lectotype): Shell medium-sized (to 8.1 mm), strong, thick, narrowly fusiform, with moderately convex whorls and attenuated, narrow, siphonal canal. Protoconch eroded, rounded, paucispiral. Whorls with narrow and slightly concave subsutural ramp, evenly convex along periphery. Axial sculpture of narrow, weakly sinuate and weakly prosocline ribs, extending from suture to suture on spire, becoming obsolete on periphery of last whorl (~ 15 ribs on penultimate and last whorls). Spiral sculpture of sharp, raised spiral cords. Cords (7–9 on spire whorls, ~ 18 on last whorl) broadly spaced adapically, with intervening spaces 1–2 times broader than cords. Cords become broader than intervening spaces along shell periphery, indistinct on siphonal canal. Aperture large (AL/SL ≈ 0.53), elliptical (AL/AW ≈ 2.0), with callus extending along parietal region and columella. Operculum oval, with terminal nucleus, shifted to left. Periostracum beige, tightly adhering. Shell beige, lighter on siphonal canal.

Gross Anatomy: Animal of the paralectotype with a broken shell (Figures 24–26, ♂) was dissected. Anatomy similar to *Falsimohnia albozonata* in most regards. Eyes large. Penis long, about the length of mantle cavity, dorsoventrally compressed, blunt distally with long but narrow seminal papilla shifted posteriorly, situated on dorsal edge of penis (Figure 26). Proboscis of moderate length, cylindrical, tapering distally. Radula (Figures 35–36) narrow (~60 μm wide), lateral teeth with broad base, elongated and weakly recurved outer edge, two strong cusps, inner cusp shorter, emanating from middle and inner portions of base. Central tooth with nearly square basal plate, its anterior edge V-shaped with indentation accommodating single medial cusp emerging from rounder posterior edge of anteriorly adjacent tooth. Lateral edges of basal plate of central tooth with thickened ridges parallel to central cusp, possibly vestiges of lateral cusps. Stomach with long posterior mixing area.

Remarks: The species is rather distinct, resembling the shell outline of *Probuccinum costatum* (Thiele, 1912), but differing from that taxon in having more numerous axial ribs on the shell, and a different radula. In *Probuccinum* the radula is typical buccinulid, with broad tricuspid central teeth and tricuspid lateral teeth that lack an elongated outer basal plate. *Falsimohnia fulvicans* appears to be rare, as the only confirmed record since the original description is that of Zelaya (2005). The radula of *F. fulvicans* is very similar to that of *F. albozonata* as is its penis morphology, both providing support for the transfer of this species to the genus *Falsimohnia*.

In his discussion of *F. albozonata*, Powell (1951:138) considered the range of this species to include South Georgia Island. Two specimens from *Discovery* station 149 that had been identified by Powell as *F. albozonata* (NHMUK 1961499) were examined (Figure 27). The similarity of these specimens to the lectotype of *F. fulvicans* indicates that they were misidentified as *F. albozonata* by Powell. Discovery station 149 is very close to Cumberland Bay, the type locality of *F. fulvicans*, and the depth is comparable to that from which a paralectotype of *F. fulvicans* was collected. In a survey of the Mollusca of the Burwood Bank, Melvill and Standen (1912:356) reported a single "imperfect, bleached specimen" that they tentatively identified as *Bela fulvicans*.

Distribution: South Georgia, and questionably Burwood Bank.

Falsimohnia minor Strebel, 1908
(Figures 28–34)

Bela anderssoni var. *minor*? Strebel, 1908: 15; Powell, 1951:59; Engl, 2012:181, pl. 73, fig. 6a.

Typhlodaphne innocentia Dell, 1990: Aldea and Troncoso, 2008: 82, fig. 64; Aldea and Troncoso, 2010: 144–145, fig. 157.

Bela polysarca var. *minor Locard*, 1897, *Bela pyrrhogramma* var. *minor* Locard, 1897, and *Bela anderssoni* var. *minor*? Strebel, 1908, were all proposed as taxa of subspecific rank (ICZN, 1999: Article 45.6.4). In our view, both *Bela polysarca* var. *minor Locard*, 1897 and *Bela pyrrhogramma* var. *minor* Locard, 1897 are *nomina nuda*, as neither name is accompanied by a description or definition of the taxon, nor by an indication (ICZN, 1999: Article 12). As *nomina nuda*, these names are not available names and do not enter into homonomy (ICZN, 1999: Article 54).

Type Locality: South Georgia Island, outer Cumberland Bay, 54°11′ S, 36°18′ W, 252–310 m, Swedischen Südpolar-Expedition, sta. 34.

Type Material: 3 syntypes, SMNH Type-1057.

Description: Shell small (to 6.5 mm), strong, moderately thick, with convex whorls and short broad canal, with shallow but distinct notch. Protoconch bulbous, eroded on all specimens. Profile of whorls between suture and shoulder slightly concave. Axial sculpture of narrow, slightly sinuous, nearly orthocline ribs (14–15 on penultimate and last whorls), extending from suture to suture on spire and suture to siphonal canal on last whorl. Spiral sculpture of low, sometimes indistinct, closely spaced spiral cords that are broader than intervening spaces. Aperture large (AL/SL = 0.54–0.61), moderately broad (AL/AW≈ 1.9), elliptical, inner lip with narrow callus on columellar and parietal portions. Operculum oval, transluscent, with terminal nucleus, shifted to left. Periostracum tightly adhering, beige to yellowish. Shell orange to brownish beige, siphonal canal and columella lighter, often whitish. Radula (Figures 33–34) [narrow (~ 55 μm wide, 1.7% of AL),] short. Lateral teeth with long basal plate with elongated outer edge and two strong, curved cusps, inner one slightly shorter. Basal plate of central tooth nearly square, with shallow

notch in anterior margin to accommodate cusp or adjacent tooth, and one strong, long medial cusp emanating from posterior edge. Small denticle on left side of cusp.

Remarks: Strebel (1908) attributed only varietal status to this taxon. We regard *Falsimophnia minor* to be a distinct species, differing from *F. andersssoni* in having more pronounced, wider and more broadly spaced axial ribs, and far less distinct spiral sculpture. The morphology of the radula, which is nearly identical to that of *F. albozonata* and *F. fulvicans*, confirms the placement of this species in the buccinulid genus *Falsimohnia*.

Conchologically, *F. minor* resembles some specimens of *Chlanidotella modesta* (Martens, 1885) from South Georgia, but differs in its smaller shell size and radular morphology. In *C. modesta* the lateral teeth have 4–5 cusps and the central tooth bears three distinct cusps of similar size (Powell, 1951: fig. L80; unpublished observations).

Distribution: South Georgia, Bellinghausen Sea, Peter I Island, 90–310 m.

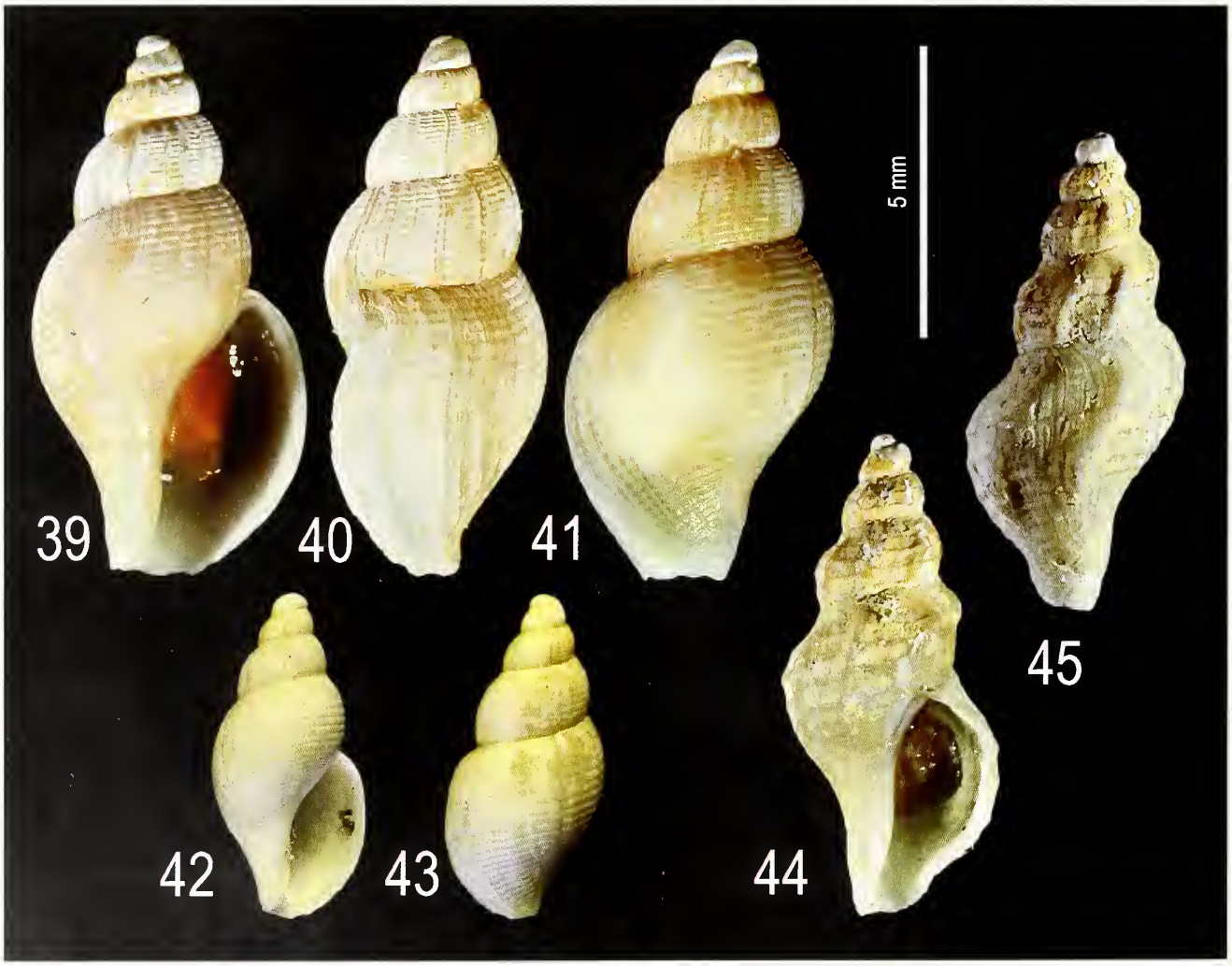
***Falsimohnia anderssoni* (Strebel, 1908)**
(Figures 39–41)

Bela anderssoni Strebel, 1908: 14–15, Taf. 2, fig. 24 a–d; Mellvill and Standen, 1912:355; Powell, 1951: 56; Engl, 2012:180–181, pl. 73, fig. 6b.

Type Locality: SE of Seymour Island, 64°20′S, 56°38′W, 150 m, Swedischen Südpolar-Expedition, sta. 5.

Holotype: SMNH Type-1063.

Description: Shell small (to 9.4 mm), fusiform, thick, with evenly rounded, convex whorls and short broad canal. Protoconch bulbous, eroded. Axial sculpture of low, very narrow, slightly sinuous ribs (19 on penultimate



Figures 39–45. Species of *Falsimohnia* and *Strebela* new genus. **39–43.** *Falsimohnia anderssoni* (Strebel, 1908). **39–41.** Holotype (SMNH Type-1063) (SL 9.4 mm). **42–43.** USNM 870245, off Elephant Island, South Shetland Islands, 220–240 m. **44–45.** Type species of *Strebela* new genus: *Bela notophila* Strebel, 1908, holotype, (SMNH Type-1064), (SL 8.1 mm). (radula extracted).

whorl) most pronounced on spire whorls, and raised growth striae that are prevalent on final whorl. Spiral sculpture of low, rounded, closely spaced spiral cords (14 on penultimate whorl, ~30 on final whorl) that are wider than intervening spaces. Aperture large (AL/SL = 0.56), broadly elliptical, (AL/AW ≈ 1.9), inner lip with narrow callus on parietal and columellar portions. Operculum oval, transparent, with terminal nucleus shifted to left, about half of aperture length. Periostracum beige, peeling. Shell beige, lighter than periostracum. The radula of the holotype was not examined.

Remarks: The shell shape and sculpture of *Falsimohnia anderssoni* are similar to those of *F. albozonata* and *"Pareuthria" innocens* (Smith, 1907) with which it may be confused [see discussion for comments regarding the generic reallocation of *Pareuthria innocens*]. *Falsimohnia anderssoni* differs from typical *F. albozonata* in its uniform beige shell color. It differs from *"Pareuthria" innocens* [syntype, BMNH, illustrated by Dell (1991), fig. 301 as "holotype"] in having a broader shell with more convex whorls, a wider aperture, more prominent spiral cords and low narrow axial ribs. We take a conservative approach in recognizing *F. anderssoni* as a distinct species, but more detailed studies as additional material becomes available may reveal that it represents a variation of either *F. albozonata* or *"P. innocens"*. Some authors (eg. Castellanos and Landoni, 1993) have considered *Falsimohnia anderssoni* to be a junior synonym of *?Bela michaelseni* Strebel, 1905 from off Patagonia, although *B. michaelseni* has a more slender shell with more pronounced axial ribs. However, there is little overlap between the gastropod fauna occuring within Antarctic Convergence and that of the Magellanic Province, even at the generic level (e.g., Harasewych et al., 2000; Harasewych and Kantor, 2004). Species originally believed to have a broad range spanning both Magellanic and Antarctic regions, generally on the basis of convergent shell morphology, are often shown to represent taxa referable to different genera and/or families when examined anatomically.

The geographic range of this species is extented to include the South Shetland Islands based on a specimen (USNM 870245) in the Smithsonian collections (Figures 42–43).

Distribution: SE of Seymour Island and Elephant Island, South Shetland Islands, 150–240 m.

DISCUSSION OF THE GENUS *FALSIMOHNIA*

We had earlier speculated (Harasewych and Kantor, 2004:42) that, based on opercular and radular morphology, *Antarctodomus okutanii* Numanami, 1996 may be referable to *Falsimohnia*, a view that was adopted by Engl (2012:145). Differences in radular morphology between *Antarctodomus okutanii* and *Falsimohnia albozonata*, the type species of *Falsimohnia*, most notably the lack of a long, tapered outer edge of the lateral teeth of *A. okutanii* as well as the broader placement of the cusps on the lateral teeth in this species, indicate to us that more research is needed for an accurate generic placement for this taxon.

Among the species described by Strebel (1908) as *Bela*, *B. notophila* Strebel, 1908 has been attributed to *Lorabela* (Powell, 1951; Zelaya, 2005) or conservatively retained in *Bela* (Engl, 1912). As with the species discussed above, the assignment of *Bela notophila* to the Conoidea has never been questioned. However, an examination of the radula obtained from the holotype of this species (Figures 37–38) undoubtedly places it within Buccinoidea. This taxon differs from all other Antarctic Buccinoidea in having a shell with axial sculpture of sinuous broadly spaced prosocline ribs. It is superficially similar to species of *Lorabela*, to which it was attributed by Powell (1951) when he established the genus *Lorabela*. The unique combination of radular and shell characters in this species necessitates the description of a new genus to include this species.

Genus *Strebela* new genus

Type Species: *Bela notophila* Strebel, 1908.

Description: Shell small, (to 8 mm), strong, thick, fusiform, with convex whorls slightly angulated at shoulder, attenuated broad siphonal canal. Protoconch paucispiral, smooth. Axial sculpture of wide, broadly spaced, strongly prosocline ribs (8 on last whorl). Spiral sculpture of few low sharp cords. Aperture moderately broad, elliptical (~ ½ shell length). Operculum small, oval, with terminal nucleus. Radula with long bicuspid lateral teeth and unicuspid central tooth with nearly square basal plate.

Remarks: This new genus differs from *Falsimohnia* in having a shell with a distinct, angulated shoulder, pronounced, widely spaced and strongly prosocline axial ribs, stronger and fewer spiral cords, and a well demarcated siphonal canal. The lateral teeth of the radula of *Strebela* have a thin basal plate, and two thin cusps that are broadly spaced, emanating from the inner and outer ends of the basal plate. Lateral teeth of *Falsimohnia* are or comparable length but much thicker and stouter. The two cusps are broader, and emanate from near the center and inner ends of the basal plate, which has a tapering outer edge.

Etymology: This new genus honors Hermann Strebel in recognition of his pioneering studies of Antarctic and subAntarctic Mollusca collected by the Swedish Antarctic Expedition (1901–1903). It is a combination of the name Strebel with the genus name *Bela*, to which he originally assigned the type species.

Strebela notophila (Strebel, 1908)

(Figures 37–38, 44–45)

Bela notophila Strebel, 1908: 20–21, Taf. 2, fig. 28 a–d; Engl, 2012:181, pl. 73, fig. 5.

Lorabela notophila—Powell 1951: 171, fig. N, 144; Zelaya, 2005: 128.

Type Locality: South Georgia, outer Cumberland Bay, 54°11′S, 36°18′W, 252–310 m, Swedischen Südpolar-Expedition, sta. 34.

Holotype: SMNH Type-1064

Description: Shell medium-sized (to 8.1 mm), strong, thick, fusiform, with convex whorls, angular shoulder, and attenuated siphonal canal slightly recurved to left, demarcated by a shallow notch. Protoconch broken in holotype. Whorl profile below suture slightly concave on penultimate and last whorls. Axial sculpture of pronounced, wide, broadly spaced, sinuous, strongly prosocline ribs (8 on last whorl) that extend from suture to suture on spire, becoming obsolete on last whorl at transition to siphonal canal. Spiral sculpture of low, narrow, widely spaced, well-defined cords (4 on penultimate whorl, 7 on the last whorl), absent on subsutural rim, distinct on the shell periphery, nearly obsolete on the siphonal canal. Aperture elongated (AL/SL ~ 0.47), narrow (AW/AL ~ 0.40), elliptical, with narrow callus along parietal and columellar regions. Siphonal canal well defined, anal sinus not pronounced. Operculum small (~ 0.5 AL), thick, ovate, with terminal nucleus shifted to left. Shell beige in color, siphonal canal whitish. Radula (Figures 37–38) narrow (~ 80 µm wide, 2.1% of AL). Lateral teeth with long, thin basal plate, two narrow, broadly spaced curved cusps (one at each end of the basal plate), inner one slightly shorter. Basal plate of central tooth nearly square, weakly notched anteriorly, with one thin, long, medial cusp emanating from posterior edge.

Distribution: South Georgia, 97–310 m.

Remarks: Powell (1951: fig. 114) illustrated the protoconch of this species, showing it to be smooth and paucispiral.

DISCUSSION

Within the Neogastropoda, a number of taxa unrelated to Conoidea were originally described in genera belonging to one of the "turrid" families on the basis of convergent shell morphology, among them species later found to belong to the genera *Exilia* (Ptychatractidae), *Antimitra* (Buccinidae), and *Daphnellopsis* (Muricidae). Conversely, some taxa originally described as buccinoideans have been shown to be referable to Conoidea when their anatomy was examined (e.g., Kantor and Harasewych, 1999).

Conchologically the species transferred here to *Falsimohnia* are similar to several Antarctic species that have been attributed to *Pareuthria* Strebel, 1905. They share a similar elongate-oval shell with a large, smooth protoconch and weak axial sculpture.

The genus *Pareuthria* Strebel, 1905, contains 20 species [WoRMS (Bouchet and Rosenberg, 2012)], of which only five [*P. innocens* (Smith, 1907), *P. plicatula* Thiele, 1912, *P. valdiviae* (Thiele, 1925), *P. turriformis* Egorova, 1982; *P. hoshiaii* Numanami, 1996], have been recorded within the Antarctic Convergence. The majority of the species of *Paraeuthria*, including the type species (*Fusus plumbeus* Philippi, 1844, by subsequent designation, Tomlin, 1932) are limited to the Magellanic Province. Radulae of the type species *Pareuthria plumbeus* (G. Pastorino, personal communication), and of two other Magellanic species, *P. fuscata* (Bruguière, 1789) and *P. venustula* Powell, 1951 (Powell, 1951: figs. 69, 70), have a broad central tooth with three cusps that are similar in size, and lateral teeth with two cusps (outer cusp longer) that lack a lateral extension along the outer margin of the basal plate.

Pareuthria innocens (Smith, 1907), a species with its type locality in the Ross Sea (Hut Point, McMurdo Sound, in 45–54 m) and with a circum-Antarctic distribution at depths of 6 to 549 m, was originally described in the conoidean genus *Thesbia* Jeffreys, 1867. It was subsequently transferred to the genus *Pareuthria* on the basis of its buccinoidean radula by Thiele (1912: 207), who provided an illustration (Thiele, 1912: pl. 16, fig. 22) that showed bicuspid lateral teeth and a tricusip central tooth. Egorova (1982: fig. 50) showed this species to have a central tooth with a single, median cusp. Hain (1990: 55) noted the differences in these figures, and provided an SEM image of the radula from a specimen he attributed to *P. cf. innocens* (Hain, 1990: pl. 22, fig. 7) in which the central tooth has a single, median cusp, but lateral teeth have two thin cusps situated at the ends of a basal plate that lacked a lateral extension. Numanami (1996: fig. 121C) published a SEM of the radula that clearly depicts a central tooth that is narrow, with a single, median cusp that is flanked by small denticles. The lateral teeth have two thick cusps as well as outer lateral projections. These reports indicate that either there is great morphological variability in the radula of this taxon, or that specimens representing more than one species contributed to these observations.

Pareuthria plicata Thiele, 1912, was described from the Davis Sea (Gauss station, in 385 m) and differentiated from *P. innocens* on the basis of shell sculpture. Engl (2012: 149) noted that this species was based on 24 variable syntypes, and designated a lectotype (Engl, 2012: pl. 54, fig. 3a). Hain (1990: pl. 22, fig. 8) published a SEM of the radula of a specimen identified as *P. cf. plicata* that was very similar to his image of the radula of *P. cf. innocens*. The squarish basal plate and long, medial cusp of the central tooth were more prominent, while the lateral teeth also had two, widely separated cusps that lacked outer lateral projections.

Pareuthria hoshiaii Numanami, 1996, is presently known only from its holotype, collected at Günnerus Bank near Syowa Station (Queen Maud Land) at 288 m. Its radula (Numanami, 1996: fig. 125D) has a central cusp with a single, broadly triangular cusp flanked by one or more pronounced denticles on each side. Lateral teeth have two thick cusps and an outer lateral projection.

Two additional species attributed to *Pareuthria*, *Enthria* (*Pareuthria*) *valdiviae* Thiele, 1925, from unspecified depths (Valdivia Station 160) off Kerguelen Island, and *Pareuthria turriformis* Egorova, 1982, from off the Shackleton Ice Shelf, Davis Sea at depths of 460 m, were described solely on the basis of shell morphology, and their radulae remain unknown.

Of the five species attributed to the genus *Pareuthria* that occur within the Antarctic Convergence for which radular morphology is known, it is clear that the radulae of *Pareuthria innocens* and *P. hoshiaii* differ from that of *P. plumbeus*, the type species of the genus. They more closely resemble the radulae of species of *Falsimohnia*, including *F. albozonata*, the type species, most notably in having a central tooth with a squarish basal plate and single prominent medial cusp (that may be flanked by denticles) as well as lateral teeth with a long basal plate with a tapering outer edge, and two thick cusps along the inner 2/3 of the tooth. We therefore transfer the taxa *Pareuthria innocens* (Smith, 1907) and *P. hoshiaii* Numanami, 1996 to the genus *Falsimohnia*. The resulting binomina are *Falsimohnia innocens* (Smith, 1907) **new combination** and *Falsimohnia hoshiaii* (Numanami, 1996) **new combination.**

The new genus *Strebela* is characterized by radula similar to that of *Falsimohnia*, but differs in having a central tooth with a squarish basal plate that appears thinner, with less well defined lateral edges, a more shallowly concave anterior that lacks an indentation for the cusp of the anteriorly adjacent tooth, and a thinner median cusp emerging from the posterior tooth margin. The lateral teeth have a narrower basal plate with two much thinner and longer cusps that are broadly spaced. The outer cusp emerges from the outer margin of the lateral tooth, which lacks the lateral projection.

A radula with this morphology was reported for *Pareuthria plicatula* [Hain, 1990: pl. 22, fig. 8 (as *Pareuthria cf. plicatula*); Numanami, 1996: fig. 123D], as well as for a specimen identified as *Parenthria cf. innocens* (Hain,1990: pl. 22, fig. 7). However, there are conspicuous differences in shell morphology between *Strebela notophila* (strongly shouldered shell with 8 prominent, sinuous and strongly prosocline axial ribs and pronounced, widely spaced spiral cords) and *Parenthria plicatula* (shell with rounded shoulder, ~ 40 thin, weakly sinuous, nearly orthocline axial ribs and lack of pronounced spiral sculpture). The appropriate generic allocation of *"Pareuthria" plicatula* is not yet clear, but major differences in radular morphology exclude it from the genus *Parenthria*.

The remaining two species from within the Antarctic convergence that have been attributed to *Parenthria* are known only from their shell morphology. *Pareuthria valdiviae* (Thiele, 1925), from Kerguelen Island was collected with *Falsimohnia albozonata*, which it resembles in shell morphology, but has more pronounced axial striae and lacks the whitish band across the periphery. *Pareuthria turriformis* Egorova, 1982 from the Ross Sea, was attributed to the genus with doubts, as it differs in shell morphology from both the Magellanic species of *Parenthria* and from *Falsimohnia*.

A review of the buccinoidean genera of the Antarctic and Magellanic regions (Harasewych and Kantor, 2004: Appendix 1) revealed only three genera that are represented by species in both regions: *Metenthria* Thiele, 1912, *Pareuthria*, and *Falsitromina* Dell, 1990. Results of the present study dispute the occurrence of the genus *Parenthria* within the Antarctic Convergence, and suggest that both *'Pareuthria' valdiviae* and *'P.' turriformis* will be referred to other genera when anatomical material becomes available. A more detailed study of *Metenthria* and *Falsitromina* may reveal similar biogeographic patterns.

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LITERATURE CITED

Aldea, C. and J.S. Troncoso. 2008. Systematics and distribution of shelled mollusks (Gastropoda, Bivalvia and Scaphopoda) from the South Shetland Islands to the Bellingshausen Sea, West Antarctica. Iberus 26: 43–117.

Aldea, C. and J.S. Troncoso. 2010. Molluscos del Mar de Bellingshausen (Antarctica). Feito, S.L., Vigo, 249 pp.

Bouchet P., P. Lozouet, and A.V. Sysoev. 2009. An inordinate fondness for turrids. Deep-Sea Research, 56: 1724–1731.

Bouchet P., P. Lozouet, P. Maestrati and V. Heros. 2002. Assessing the magnitude of species richness in tropical marine environments: high numbers of molluscs at a New Caledonia site. Biological Journal of the Linnean Society 75: 421–436.

Bouchet P., Yu. I. Kantor, A. Sysoev and N. Puillandre. 2011. New operational classification of the Conoidea (Gastropoda). Journal of Molluscan Studies 77: 273–308.

Bouchet, P. and G. Rosenberg. 2012. *Pareuthria* Strebel, 1905. Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=196933 [on March 13, 2013]

Castellanos, Z.J.A. and N. Landoni. 1993. Catálogo descriptivo de la malacofauna magallánica, 11. Neogastropoda Turridae. Comisión de Investigaciones Cientificas, Provincia de Buenos Aires: 1–31.

Dell, R.K. 1990. Antarctic Mollusca with special reference to the fauna of the Ross Sea. Bulletin of the Royal Society of New Zealand 27: 1–311.

Egorova, E. 1982. Biological results of the Soviet Antarctic expeditions, 7. Molluscs of the Davis Sea. Explorations of the Fauna of the Seas 26(34): 1–142.

Engl, W. 2012. Shells of Antarctica. ConchBooks, Hackenheim, 402 pp.

Hain, S.G. 1990. Beiträge zur Biologie der beschalten Mollusken (Kl. Gastropoda und Bivalvia) des Weddellmeeres, Antarktis. Berichte zur Polarforschung 70: 1–181.

Harasewych, M.G. and Yu. I. Kantor. 2004. The deep-sea Buccinoidea (Gastropoda: Neogastropoda) of the Scotia Sea and adjacent abyssal plains and trenches. The Nautilus 118: 1–42.

Harasewych, M.G., Yu. I. Kantor, and K. Linse. 2000. *Parabuccinum*, a new genus of Magellanic Buccinulid (Gastropoda: Neogastropoda), with a description of a new species. Proceedings of the Biological Society of Washington 113: 542–560.

Hedley, C. 1916. Mollusca. Australasian Antarctic Expedition 1911–1914 Scientific Reports C - Zoology and Botany 4: 1–80.

ICZN [International Commission on Zoological Nomenclature], 1999. International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature, London, xxix + 306 pp.

Kantor, Yu. I. and M.G. Harasewych. 1999. Rediscovery of the Antarctic species *Sipho gaini* Lamy, 1910 (Gastropoda: Neogastropoda) with remarks on its taxonomic position. Antarctic Research 11: 431–436.

Kantor, Yu. I. and A.V. Sysoev. 2006. Marine and brackish-water Gastropoda of Russia and adjacent countries: an illustrated catalogue. KMK Scientific Press Ltd., 371 pp +140 pls.

Locard, A. 1897. Mollusques Testacés. In: Milne-Edwards, Expéditions Scientifiques du Travailleur et du Talisman Pendant les Années 1880, 1881, 1882, 1888, Paris. 1: 1–516, pls. 1–22.

Martens, E. 1885. Vorläufige Mittheilungen über die Mollusken-fauna von Süd-Georgien. Gesellschaft Naturforschender Freunde zu Berlin, pp. 89–94.

Martens, E. von and G. Pfeffer. 1886. Die Mollusken von Süd-Georgien: nach der Ausbeute der Deutschen Station 1882–83. Jahrbuch der Hamburgischen wissenschaftlichen Anstalten 3: 65–135, pls. I–4.

Martens, E. von and J. Thiele. 1904. Die beschalten Gastropoden der deutschen Tiefsee-Expedition, 1898–99. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Especition auf dem Dampfer „Valdivia" 1898–1899. 7: 1–179, pls. 1–9.

Melvill, J.C. and R. Standen. 1912. The marine Mollusca of the Scottish National Antarctic Expedition. Part II. Being a supplementary catalogue. Transactions of the Royal Society of Edinburgh 48: 333–366, 1 pl.

Numanami, H. 1996. Taxonomic study on Antarctic gastropods collected by Japanese Antarctic research expeditions. Memoirs of the National Institute of Polar Research, series E 39: 1–244.

Powell, A.W.B. 1951. Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. Discovery Reports 26: 47–196.

Strebel, H. 1908. Die Gastropoden. Wissenschaftliche Ergebnisse der schwedischen Südpolar Expedition. 1901–1903. 6: 1–112.

Thiele, J. 1912. Die antarktischen Schnecken und Muscheln. Deutsche Südpolar Expedition 1901–1903, 13: 183–285.

Tucker, J.K. 2004. Catalog of Recent and fossil turrids (Mollusca: Gastropoda). Zootaxa 682: 1–1295.

Tucker, J.K. and M.J. Tenorio. 2009. Systematic Classification of Recent and Fossil Conoidean Gastropods. Conchbooks, Hackenheim, 296 pp.

Watson, R.B. 1882. Mollusca of the H.M.S. "Challenger" Expedition. Part XII. Journal of the Linnean Society, Zoology 16: 324–343.

Watson, R.B. 1886. Report on the Scaphopoda and Gasteropoda collected by H.M.S. Challenger during the years 1873–1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger. Zoology 15: 1–756.

Zelaya D.G. 2005. Systematics and zoogeography of marine gastropod molluscs of South Georgia. Spixiana 28: 109–139.

Aidemofusus ignotus new genus and new species, a new buccinid (Gastropoda: Neogastropoda) from the North Pacific Ocean

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ABSTRACT

Aidemofusus ignotus, a new species and genus of North Pacific buccinids is described. Shell and operculum morphology as well as general foregut anatomy are similar to several Colinae (Buccinidae) genera, while radula structure is very unusual for the family, precluding inclusion of the new genus into any recognized subfamily of Buccinidae.

Additional Keywords: Buccinidae, taxonomy, Russia, Okhotsk Sea

INTRODUCTION

Buccinoidea is a large and diverse superfamily of predatory marine gastropods, widely distributed in polar, temperate and tropical waters of the World Ocean. It encompasses several families, few of which are well defined conchologically and anatomically (Nassariidae, Melongenidae, Colubrariidae, Columbellidae) and well supported in molecular phylogenies (Oliverio and Modica, 2010). Two families, Fasciolariidae and Buccinidae were not retrieved as monophyletic in a few molecular analyses and may be paraphyletic. Buccinidae (in currently accepted sense – Bouchet and Rocroi, 2005) are especially heterogeneous, and include groups that are conchologically and anatomically very different, which is reflected in their complicated taxonomic structure. The state of the art classification presented in Bouchet and Rocroi (2005) recognizes 6 subfamilies and 11 tribes. Despite the high number of described and accepted suprageneric taxa, there remained several genera of Buccinoidea with uncertain taxonomic position, among them *Buccipagoda* Ponder, 2010, *Costaria* Golikov, 1977, and *Troschelia* Mörch, 1876. Systematics of the Buccinidae is still based mostly on conchological characters with occasional use of radulae. Relatively few buccinids have been included in molecular phylogenetic studies (e.g., Hayashi, 2005; Kosyan et al., 2009). The main reason is unavailability of properly preserved material, especially of boreal and Arctic species, vast collections of which had been accumulated over the years in European and American museums. Therefore morphology and conchology remain the principal approaches to buccinid alpha-taxonomy at the moment.

The practical needs for biodiversity studies require descriptions of new taxa, even in groups for which a robust phylogeny and classification are future goals. Many of species remain rare and probably will not be recollected in the near future.

While preparing a revision of the north-western Pacific buccinids, we found a peculiar species that cannot be confidently placed in any recognized suprageneric taxon. The combination of conchological, anatomical and radular characters preclude including it in any known genus. Therefore a new species and genus are proposed, and tentatively attributed to Buccinidae.

MATERIALS AND METHODS

The material for the study is deposited at P.P. Shirshov Institute of Oceanology, Moscow, and Zoological Institute of Russian Academy of Sciences, St. Petersburg. Standard methods were used, including manual dissection and scanning electron microscopy for examination of the radulae. Abbreviations used in the text are: AL: aperture length; D: shell diameter; H: height of the shell; h: height of the last whorl; spm: specimen; IO: P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia; ZIN: Zoological Institute, Russian Academy of Sciences; ZMMU: Zoological Museum of Moscow State University, Russia.

SYSTEMATICS

Order Neogastropoda Wenz, 1938
Family Buccinidae Rafinesque, 1815

Genus *Aidemofusus* new genus

Type Species: *Aidemofusus ignotus* new species, by original designation.

Description: Shell small, up to 25 mm in length, broadly fusiform, with low spire and moderately long, strongly recurved siphonal canal. Spiral sculpture of low, closely spaced, wavy cords, with much narrower interstices; about 12 cords on penultimate whorl and 30 on last whorl and canal. Axial sculpture of weak, low, slightly recurved ribs, about 15 on last whorl. Aperture high > ½ SL, elongate oval, strongly constricted on passing to siphonal canal. Columellar margin weakly concave, nearly straight. Columellar and parietal margins with narrow callus. Operculum with terminal nucleus, strongly turned to left, about 0.8 AL. Central tooth of radula small, with subsquare base and serrated posterior margin. Lateral teeth square, with nearly straight posterior edge with numerous (7–12) short sharp cusps. Salivary ducts form widened pouches at base of inverted proboscis.

Remarks: *Aidemofusus* can be easily distinguished by its unusual radula. It has a distant similarity to radulae of *Parancistrolepis* Azuma, 1965 in the morphology of its lateral teeth, but the central tooth is different as is the operculum. *Costaria borealis* Golikov, 1977 and *Troschelia berniciensis* (King, 1846), possess wide lateral radular teeth with multiple cusps, but the cusps are much longer and the central tooth has a different shape in these genera. Shell of *Aidemofusus* may be easily confused with shells of small-sized buccinid genera possessing axial ribs such as *Retifusus* Dall, 1916 and *Retimohnia* McLean, 1995.

Etymology: The genus name (masculine gender) derives from *aidemos* (Greek: bashful, modest), recognizing the unremarkable shell, lacking any diagnostic characters.

***Aidemofusus ignotus* new species**
(Figures 1–24, Table 1)

Description: Shell small, thick, solid, broadly fusiform, with low spire, of 5+ convex whorls (Figures 1–6). Protoconch and upper telecoconch whorls abraded in all specimens. Shell surface usually strongly eroded. Last whorl high to very high, strongly convex. Spiral sculpture of low, closely spaced wavy cords, with interstices four times narrower than cords; about 12 cords on penultimate whorl and 30 on last whorl and canal. Axial sculpture of weak, low, slightly recurved ribs, about 15 on last whorl. Aperture high, > ½ SL, elongate oval, strongly constricted on passing to siphonal canal. Outer lip usually evenly convex, sometimes flattened in middle part. Siphonal canal medium-long, broad, strongly recurved to left. Columellar margin weakly concave, nearly straight. Columellar and parietal margins with narrow callus. Shell pale in color, covered with thin yellowish-beige periostracum. Operculum (Figure 14) with terminal nucleus, strongly turned to left (almost subspiral), comprising about 0.8 AL.

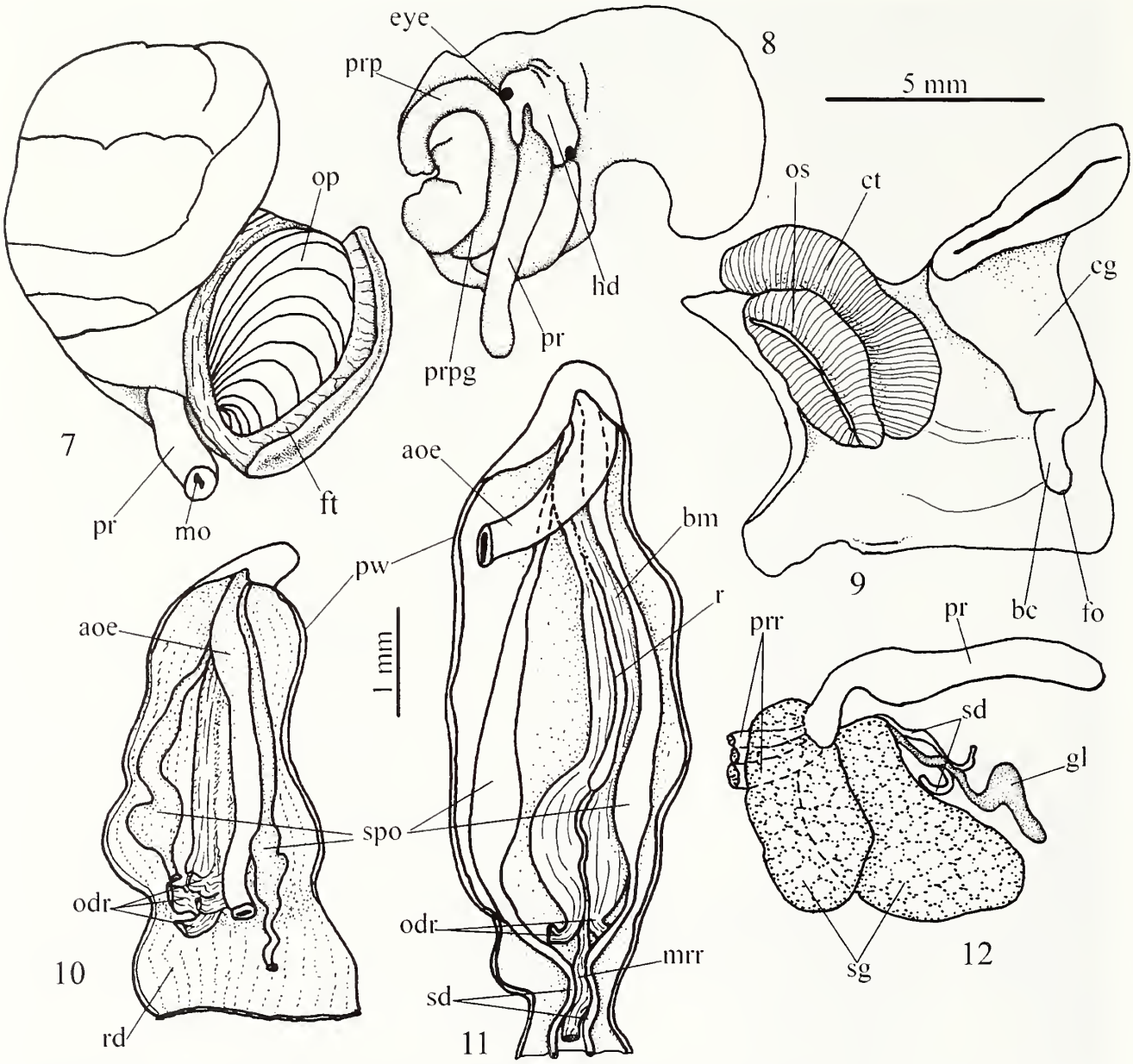
External Anatomy: Head wide, with moderately-long contracted tentacles and large black eyes on lobes at base of tentacles (Figures 8, 13). Foot contracted, with medium-wide propodium (Figure 8). Mantle length equals width, ctenidium spans 2/3 (paratype 1, Figure 9) or nearly entire mantle length, more broad in posterior part (spm. 1, Figure 15). Osphradium about ¾ (paratype 1) or ½ of ctenidium length (spm. 1). Penis of spm. 1 with large conical seminal papilla, not surrounded by fold of skin (Figure 17, **sp**). Capsule gland of paratypes 1 (Figure 9, **cg**) and 3 large, occupying about 1/3 width and almost complete length of mantle cavity. Bursa copulatrix represented by narrow moderately thick-walled tube, lined inside with multiple longitudinal folds (Figure 9, **bc**). Female orifice, a very small pore on tip of bursa copulatrix tube (Figure 9, **fo**).

Digestive System: Description based on holotype, paratype 1 and spm. 1: Proboscis short, completely (in paratype 1, Figures 8, 12) or partially everted (spm. 1, Figure 16). Proboscis retractors attached to base of proboscis (Figures 12, 16, **prr**). Salivary glands paired, long, equal to proboscis length (Figures 12, 16, **sg**). Salivary ducts very thick, widen to form salivary poaches either inside proboscis (holotype and paratype 1, Figures 10, 11, **spo**) or at mid length of anterior oesophagus, and entering proboscis along oesophagus (Figure 16, spo). In holotype and paratype 1 salivary poaches become narrow close to buccal cavity (Figure 10, 11); in spm. 1 salivary poaches wider than oesophagus, opening into buccal cavity at proboscis tip without narrowing. Buccal mass as long as proboscis in holotype (Figure 10, **bm**), about 2/3 proboscis length in paratype 1 (Figure 11, **bm**) and spm. 1. Radula sac slightly shorter than buccal mass. Radula of holotype 2.5 mm long and about 80 µm wide,

Table 1. *Aidemofusus ignotus* new species. Dimensions and gender of specimens examined in this study. AL: aperture length; D: shell diameter; H: height of the shell; h: height of the last whorl.

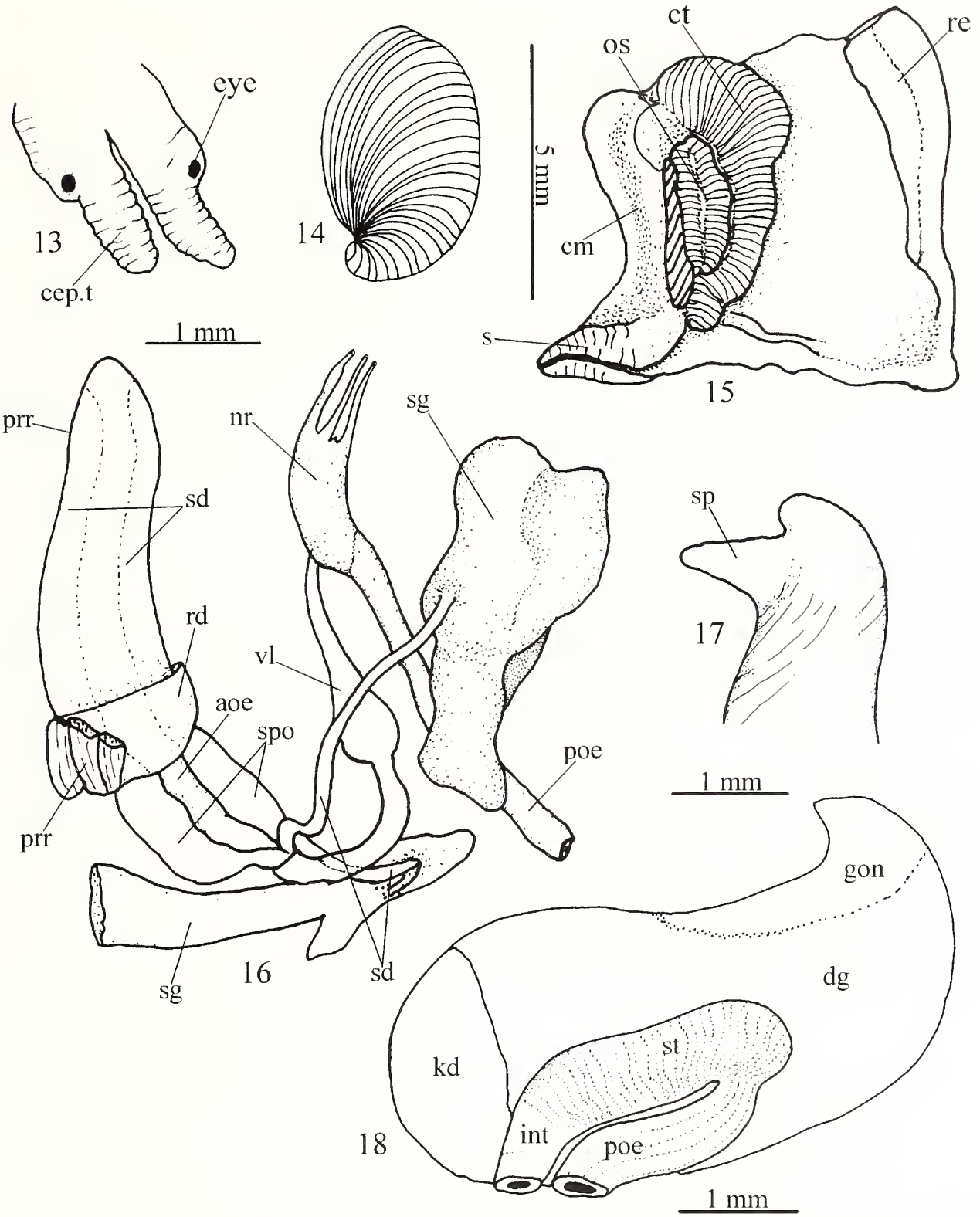
	H	h	AL	D	sex
Holotype	19.7	14.9	10.8	10.5	mature female
Paratype 1	24.9	17.7	12.1	12.7	mature female
Paratype 2	24.3	18.2	13.0	12.4	dead
Paratype 3	19.7	16.0	12.4	11.7	mature female
Paratype 4	22.5	18.0	13.2	12.7	–
Paratype 5	21.9	17.2	13.1	12.4	–
Specimen 1	21.7	17.0	12.8	11.2	mature male

Figures 1–6. Shells of *Aidemofusus ignotus* new species. **1.** Holotype. **2.** Paratype 1. **3.** Paratype 2. **4.** Paratype 3. **5.** Paratype 4. **6.** Spm. 1, from the western Bering Sea, 1960 m.

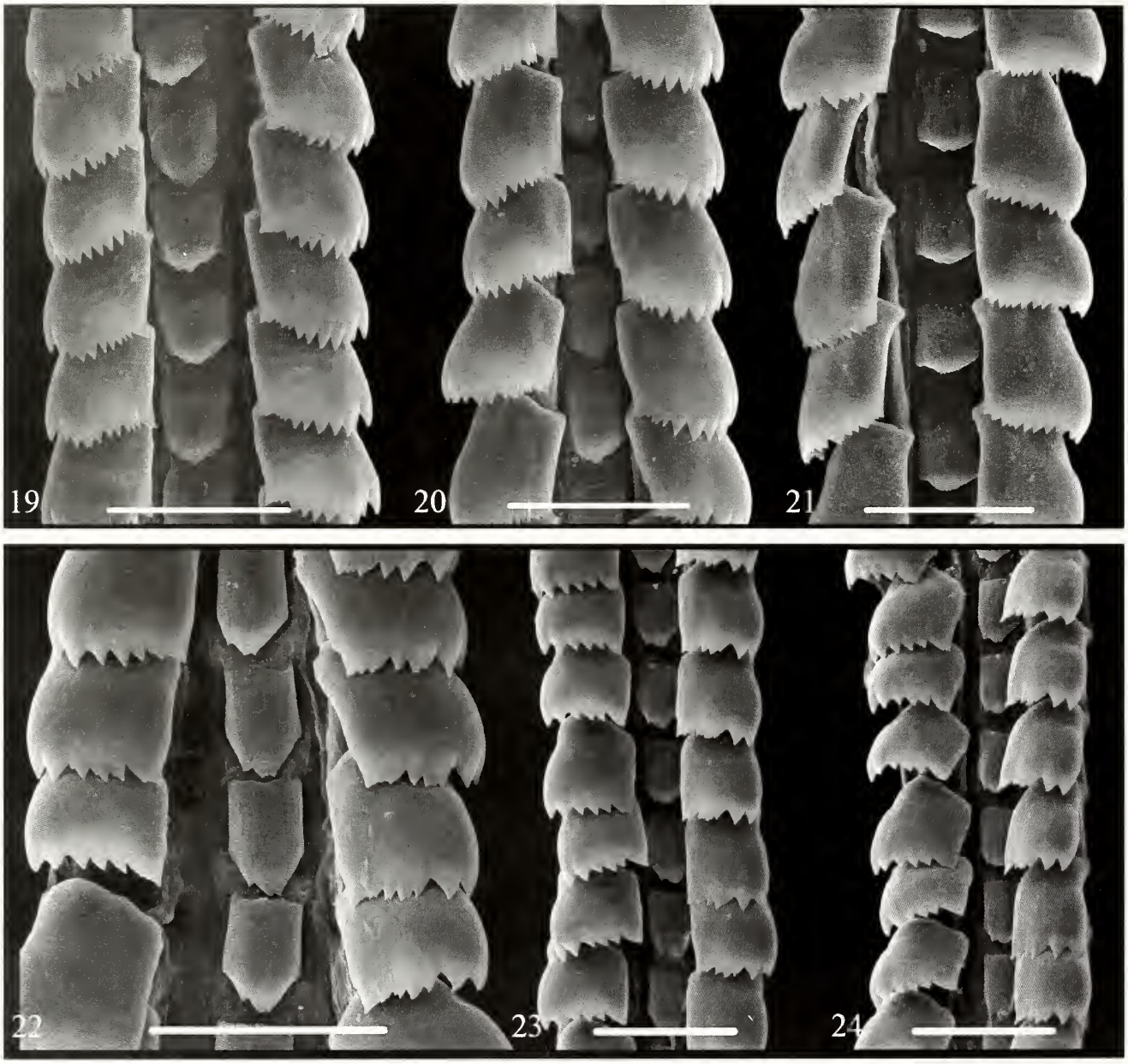


Figures 7–12. Anatomy of *Aidemofusus ignotus* new species. **7–9, 11–12.** Paratype 1. **10.** Holotype. **7.** Soft parts, ventral view. **8.** Cephalopodium, dorsal view. **9.** Mantle. **10.** Opened proboscis, holotype. **11.** Opened proboscis, paratype 1. **12.** Foregut. Abbreviations: **aoe,** anterior oesophagus; **bc,** bursa copulatrix; **bm,** buccal mass; **cg,** capsular gland; **ct,** ctenidium; **eye,** eye; **fo,** female orifice; **ft,** foot; **gl,** gland of Leiblein; **hd,** head; **mo,** mouth opening; **mrr,** medial radular retractor muscle; **odr,** odontophoral retractor muscles; **op,** operculum; **os,** osphradium; **pr,** proboscis; **prp,** propodium; **prpg,** propodial groove; **prr,** proboscis retractors; **pw,** proboscis wall; **r,** radula; **rd,** rhynchodaeum; **sd,** salivary duct; **sg,** salivary gland; **spo,** salivary poaches.

consisting of 108 rows of teeth (Figures 19–20). Central tooth small, with subsquarish base and trapezoidal, serrated posterior margin. Lateral teeth are almost of the same height and twice the width of the central tooth, square, with about 8 equal short sharp cusps in the right and 11 in the left longitudinal tooth row, some bearing additional smaller denticles. Number of cusps and shape of denticles differs from row to row. Radula of paratype 1 is 3 mm long and about 75 µm wide, consisting of 98 rows of teeth (Figure 21); central tooth is the same as above described, lateral teeth bear about 13 and 8 extremely short cusps respectively. Radula of spm. 1 is 3 mm long and about 75 µm wide, consisting of 112 rows of teeth with laterals bearing about 7 rather long cusps in each longitudinal row (Figures 22–24). Gland of Leiblein very small in paratype 1 (Figure 12, **gl**) and not found in spm.



Figures 13–18. Anatomy of *Aidemofusus ignotus* from the western Bering Sea, 1960 m. **13.** Head. **14.** Operculum. **15.** Mantle. **16.** Foregut. **17.** Distal part of penis. **18.** Stomach, general view. Scale bar 1 mm. Abbreviations: **aoe,** anterior oesophagus; **cep.t,** cephalic tentacles; **cm,** columellar muscle; **et,** ctenidium; **dg,** digestive gland; **eye,** eye; **gon,** gonad; **int,** intestine; **kd,** kidney; **nr,** nerve ring; **os,** osphradium; **poe,** posterior oesophagus; **pr,** proboscis; **prr,** proboscis retractors; **rd,** rhynchodaeum; **re,** rectum; **s,** siphon; **sd,** salivary duct; **sg,** salivary gland; **sp,** seminal papilla; **spo,** salivary poaches; **st,** stomach; **vl,** valve of Leiblein.



Figures 19–24. Radulae of *Aidemofusus ignotus* new species. 19, 20. Holotype. 21. Paratype 1. 22–24. Specimen from the western Bering Sea, 1960 m. Scale bar 50 μm.

1 (due to poor fixation). Valve of Leiblen large, swollen, situated immediately anterior to nerve ring at proboscis base in paratype 1 and at a distance from nerve ring in spm. 1 (Figure 16, **vl**). Nerve ring medium large. Posterior oesophagus slightly wider than anterior. Stomach (Figure 18, **st**) spans about 1/4 of whorl, parallel to its longitudinal axis and bordering kidney (Figure 18, **kd**). Posterior mixing area absent. Stomach walls lined with multiple low transverse folds; posterior oesophagus lined with tall longitudinal folds. More detailed study was not possible because of poor fixation.

Remarks: Shells of type specimens are strongly eroded (paratype 5 lacks any spiral sculpture and not figured). Specimens from the Sea of Okhotsk (holotype, paratypes 1 and 2) differ slightly from specimens from the Bering Sea (paratypes 3–5 and spm.1) in having a higher spire. In specimens from the Okhotsk Sea, the shell periphery is in the middle part of last whorl, while in specimens from the Bering Sea the shell periphery is in the upper third of the last whorl and the shells are more globose. We consider these distinctions as resulting from intraspecific geographic variability. A specimen

from the western Bering Sea (Figure 6), collected in 1960 m is similar conchologically to types, but we did not include it in the type series because of the very large bathymetric differences of habitat, and attribute it to the new species conditionally.

Type locality: 50°51′ N 156°01′ E, Okhotsk Sea, depth 94 m.

Type Material: Holotype ZMMU LC 39504, Okhotsk Sea, off Shumshu Island, northern Kurile Islands, R/V Vityaz, sta. 2821, 50°51′ N, 156°01′ E, depth 94 m, 27 May 1954. Paratypes 1,2 ZMMU LC 39505, sta. 2817, 51°00′ N, 156°09′ E, depth 114 m, 26 May 1954. Paratypes 3–5: ZIN 61623, Northern Bering Sea, R/V Dalnevostochnik sta. 26, 64°45.5′ N, 169°35.5′ W, 47 m, 17 Aug. 1932, coll. Ivanov, Makarov.

Other Material Examined: IO, Western Bering Sea, R/V Vityaz, sta. 1030, 60°24.7′ N, 173°46.9′ E, depth 1960 m, 16 Oct. 1951 (1 live spm).

Distribution: Northern Bering Sea, Northern Kurile Islands, 47–1960 m.

Etymology: Species name originates from *ignotus* (Lat. unknown, strange), to reflect its unusual radula morphology.

DISCUSSION

The systematics of the large family Buccinidae is very complicated and not fully resolved. There are several genera that can be allocated to either Buccinidae or Fasciolariidae (e.g., *Costaria*, *Troschelia*), and the attempts to resolve their phylogeny have been unsuccessful, which resulted in a paraphyletic Buccinidae (Kosyan et al., 2009). The shell of *Aidemofusus ignotus* can be easily confused with other small-sized buccinids possessing axial ribs (e.g., *Retifusus* and *Retimohnia*). A distinctive character of foregut of the new species are the extremely wide salivary ducts that form thick-walled pouches. Salivary pouches were found in several small-sized buccinid species in the subfamily Colinae: *Pararetifusus kosugei* Kosyan 2006, *Retifusus roseus* (Dall, 1877), *Colus latericeus* (Møller, 1842), and *Retimohnia* sp. (Kosyan, 2006, 2007; Kosyan and Kantor 2009), but these all have thin walls. In specimens of *R. roseus* with an inverted proboscis, salivary pouches are usually posterior to the proboscis base. During proboscis evertion, the salivary pouches move inside and become more elongated. Transverse sections of salivary ducts of *R. roseus* show the presence of a rather thick outer layer of circular muscle fibers (Kosyan, 2007); this indicates the possibility of peristaltic contractions. The function of the pouches is not clear. They are probably used for accumulation and quick delivery of large amounts of saliva during feeding.

The radula structure in the new genus is very unusual for Buccinidae. In *Parancistrolepis*, the lateral teeth are somewhat similar, having numerous small cusps (although longer than in the new genus), but the central tooth bears 3 or 4 distinct cusps, and the breadth of base of central tooth exceeds length (Habe, 1972). In *Costaria borealis* from the Kurile Islands and *Troschelia berniciensis* (North Atlantic), lateral teeth have multiple cusps, but the cusps are much longer, and the teeth are much broader (Golikov, 1977; Bouchet and Warén, 1985). The central teeth of these taxa have only one or two cusps that are distinct and relatively much longer cusps than those in *Aidemofusus*. Cuspless central teeth are also found in the family Columbellidae (e.g., Bandel, 1984).

The above discussion indicates that the taxonomic position of *Aidemofusus ignotus* remains uncertain. Conchologically it can be attributed to the subfamily Colinae, but its radula precludes its inclusion in any recognized suprageneric taxon.

ACKNOWLEDGMENTS

The authors are very grateful to Dr. A.V. Gebruck, Dr. E.M. Krylova, and T.A. Savilova from IO RAN (Moscow, Russia) and Dr. B.I. Sirenko and R.A. Pikalova from ZIN RAN (Saint-Petersburg, Russia) for access to the collections in their care and for assistance while working with molluscan collections and archives. Many thanks to N.N. Surovenkova from IPEE RAN (Moscow, Russia) who much helped with scanning electron microscopy of the radulae, and to Dr. M.G. Harasewych for valuable corrections of the manuscript. The study was supported by RFBR grants No. 11-04-01284-a and 12-05-00082-a.

LITERATURE CITED

Azuma, M. 1965. On the radulae of *Ancistrolepis kinoshitai* (Kuroda) and *A. trochoideus ovoideus* Habe et Ito. Venus 24: 127–129.

Bandel, K. 1984. The radulae of Caribbean and other Mesogastropoda and Neogastropoda. Zoologische Verhandelingen 214: 1–188, 122 pl.

Bouchet, P. and J.-P. Rocroi. 2005. Classification and nomenclator of gastropod families. Malacologia 47: 1–397.

Bouchet, P. and A. Warén. 1985. Revision of the Northeast Atlantic bathyal and abyssal Neogastropoda excluding Turridae (Mollusca, Gastropoda). Bollettino Malacologico, Supplemento 1, 296 pp.

Dall, W.H. 1877. Preliminary descriptions of new species of mollusks from the northwest coast of America. Preprint of Proceedings of Californian Academy of Sciences 7: 1–6. [Volume 7 never published].

Dall, W.H. 1916. Prodrome of a revision of the chrysodomoid whelks of the boreal and arctic regions. Proceedings of the Biological Society of Washington 29: 7–8.

Golikov, A.N. 1977. Investigation of prosobranchs of the family Fasciolariidae in temperate waters. Investigations of marine fauna 21(29): 102–104. [In Russian].

Habe, T. 1972. Notes on the genus *Parancistrolepis* Azuma (Buccinidae). The Nautilus 86: 51–52.

Hayashi, S. 2005. The molecular phylogeny of the Buccinidae (Caenogastropoda: Neogastropoda) as inferred from the

complete mitochondrial 16S rRNA gene sequences of selected representatives. Molluscan Research 25: 85–98.

King, W. 1846. An account of some shells and other invertebrate forms found on the coast of Northumberland and of Durham. Annals and Magazine of Natural History 18: 233–251.

Kosuge, S. 1967. On the transfer of *"Phymorhynchus?" tenuis* Okutani, 1966 to the family Buccinidae. Venus 25: 59–64.

Kosyan, A.R. 2006. Two new species of the genus *Pararetifusus* Kosuge, 1967 (Buccinidae: Colinae), with notes on the morphology of *Pararetifusus tenuis* (Okutani, 1966). Ruthenica 16: 5–15.

Kosyan, A.R. 2007. Morphology and taxonomy of the gastropods of the subfamily Colinae (Neogastropoda: Buccinidae) of the Far-East seas of Russia PhD dissertation. A.N. Severtzov Institute of Ecology and Evolution, Russian Ac. Sci., Moscow, 223 pp. [In Russian].

Kosyan, A.R., M.V. Modica, and M. Oliverio. 2009. The anatomy and relationships of *Troschelia* (Neogastropoda: Buccinidae): New evidence for a closer fasciolariid-buccinid relationship? The Nautilus 123: 95–105.

Kosyan, A.R., Yu. I. Kantor, Yu.I. 2009. Phylogenetic analysis of the subfamily Colinae (Neogastropoda: Buccinidae) based on morphological characters. The Nautilus 123: 83–94.

McLean, J.H. 1995. Four new genera for Northeastern Pacific prosobranch gastropods. The Nautilus 108: 39–41.

Møller, H.P.C. 1842. Index Molluscorum Groenlandia. Naturhistorisk Tidsskrift 1 4(1): 76–97.

Mörch, O.A.L. 1876. Description d'espèces nouvelles. Journal de Conchiliologie 24: 368–374.

Oliverio, M. and M.V. Modica. 2010. Relationships of the haematophagous marine snail *Colubraria* (Rachiglossa: Colubrariidae), within the neogastropod phylogenetic framework. Zoological Journal of the Linnean Society 158: 779–800.

Ponder, W.F. 2010. A replacement name for *Kapala* Ponder, 1982 (Gastropoda: Buccinidae). Molluscan Research 30: 56.

Rafinesque, C.S. 1815. Analyse de la nature ou tableaude l'univers et des corps organizes. Palerme, 223 pp.

Röding, P.F. 1798. Museum Boltenianum. Pars secunda continens Conchylia, etc. Hamburg, 199 pp.

Wenz, W. 1938–1944. Teil 1: Allgemeiner Teil und Prosobranchia. In: Schindewolf, O.H. (ed.) Handbuch der Paläozoologie Band 6 Gastropoda. Verlag Gebrüder Bornträger, Berlin, xii + 1639 pp.

A new species of *Striostrea* (Bivalvia: Flemingostreidae) from the upper Pliocene and lower Pleistocene strata of Florida, USA

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ABSTRACT

Faunal studies of the Tamiami and Caloosahatchee formations (upper Pliocene to lower Pleistocene) in southern peninsular Florida have revealed a new crassostreine oyster, *Striostrea paucichomata* Bolton new species. Although similar in appearance, this bivalve differs from *Crassostrea virginica* (Gmelin, 1791) by having weakly developed chomata (not visible in about 30% of the specimens examined), the right valve having a riblet-bearing surficial layer (visible only on exceptionally well-preserved specimens), and an adductor muscle attachment that is situated more dorsally. The geology of the type area of *S. paucichomata* in northern Sarasota County, and a stratigraphic nomenclatural history of the Tamiami and Caloosahatchee formations are reviewed. A key to Cenozoic crassostreine oysters known from the southeastern United States is also provided. The following new generic placements are proposed for four previously named species: *Myrakeena sculpturata* (Conrad, 1840) **new combination**, *Myrakeena lawrencei* (Ward and Blackwelder, 1987) **new combination**, *Myrakeena greeni* (Ward, 1992) **new combination**, *Undulostrea locklini* (Gardner, 1945) **new combination** and *Striostrea cahobasensis* (Pilsbry and Brown, 1917) **new combination**.

Additional Keywords: Mollusca, Crassostreinae, *Striostrea gigantissima* (Finch, 1824), *Conradostrea*, Fossil

INTRODUCTION

Investigations of two mounds of construction fill in Manatee County, Florida (the fill probably originated from northern Sarasota County quarries) in 1996 and 1998, which contained molluscan fauna typical of the Pinecrest beds of the Tamiami Formation (upper Pliocene to lower Pleistocene), revealed a crassostreine oyster species different from *Crassostrea virginica* (Gmelin, 1791) and herein described as *Striostrea paucichomata* Bolton new species. A review of published faunal lists for crassostreine oysters from the Pliocene and early Pleistocene of Florida found only *C. virginica* (see Mansfield, 1932, 1939; Olsson and Harbison, 1953; DuBar, 1958, 1962; Stanley, 1986; Campbell, 1993). Examination of the extensive fossil collections at the Florida Museum of Natural History (FLMNH) found that *S. paucichomata* is a common component of the Tamiami Formation and also present in the Caloosahatchee Formation (lower Pleistocene) in southern peninsular Florida. All of the type, figured and referred specimens are deposited in the University of Florida, Florida Museum of Natural History, Invertebrate Paleontology Collection and are cataloged with the prefix UF and a lot number.

Specimens of *Striostrea paucichomata* found in the Tamiami Formation were commonly found in association with the oysters *Hyotissa haitensis* (G.B. Sowerby I, 1850), *Ostrea compressirostra* Say, 1824, and *Myrakeena sculpturata* (Conrad, 1840) **new combination**. Oysters less commonly associated with *S. paucichomata* were *Undulostrea locklini* (Gardner, 1945) **new combination**, *C. virginica*, *Cubitostrea coxi* (Gardner, 1945), and *Dendostrea frons* (Linnaeus, 1758). *Myrakeena sculpturata* was placed in the genus *Conradostrea* Ward and Blackwelder, 1987 along with *Myrakeena lawrencei* (Ward and Blackwelder, 1987) **new combination** and *Myrakeena greeni* (Ward, 1992) **new combination**. The diagnostic shell characters of *Conradostrea* are the same as those of *Myrakeena* Harry, 1985 and therefore *Conradostrea* should be considered a junior synonym of *Myrakeena*. The shell morphology of *U. locklini* is consistent with the description of *Undulostrea* Harry, 1985 and therefore should be included in that genus. *Myrakeena* and *Undulostrea* have similar spatial and temporal distributions as the genus *Placunanomia* Broderip, 1832 (Anomiidae Rafinesque, 1815). These three genera inhabited the eastern Pacific and western Atlantic in the Pliocene and became extirpated from the western Atlantic by the middle of the Pleistocene with one or two species still extant in the eastern Pacific [*Myrakeena angelica* (Rochebrune, 1895); *Undulostrea megodon* (Hanley, 1846); *Placunanomia cumingii* Broderip, 1832; *Placunanomia panamensis* Olsson, 1942].

Stenzel (1971: N1128) in his revision of the oysters stated that fossil crassostreines (as nonincubatory genera within the subfamily Ostreinae) "are recognized by their left valve umbonal cavity and similarity to living *Crassostrea*". Harry (1985: 149) in his revision of the living oysters recognized the subfamily Crassostreinae proposed by Torigoe (1981) and characterized the shells as

"medium to large size, usually elongated dorsoventrally, occasionally subcircular. The left valve is usually deeply concave, and the right one is usually nearly flat. Shell plications are usually limited to the left valve, often indifferently developed or absent. The early part of the right valve exterior has continuous growth of the outer shell layer, and later it often forms fragile, appressed, overlapping lamellae, but the outer surface is frequently eroded during life, obliterating the sculpture. The chomata are ostreine, or absent. The muscle scars tend to be more darkly colored than the surrounding shell, in one or both valves."

Stenzel (1971) and Harry (1985) listed the presence of a riblet-bearing surficial layer on the right valve and the presence of chomata as characters that separate *Striostrea* from *Crassostrea*. Stenzel (1971) described the riblet-bearing surficial layer as: "This layer is thin and delicate and flakes off readily. In fossil species, only a few exceptionally well-preserved specimens retain it on the outer face of the right valve (see Fig. 107,1c). Commonly the layer is dark-colored because it is either made entirely of conchiolin or is a prismatic calcite layer rich in conchiolin. Riblets are restricted to this surficial layer, and the immediately underlying, more calcareous and lighter-colored layer shows a faint trace of them at best. Because of its delicate consistency the riblet-bearing layer is better preserved in very young and still fragile oyster shells and dehisces in older individuals. Old individuals may show riblets only on the marginal conchiolin fringes." (p. N979) and "Right valve covered by many thin, readily dehiscent, conchiolin-rich imbricating layers that have prismatic shell structure and carry on their tops many narrow (1.3 mm. or less wide) dichotomous flat-topped radial riblets separated by narrower interspaces, riblets converging and diverging irregularly from place to place, producing shaggy appearing surface, becoming less abundant and less prominent in later growth stages." (p. N1136).

Stenzel (1971: N979) provided *Striostrea alabamiensis* (I. Lea, 1833) as an example of an extinct species of *Striostrea* based on the description and illustrations in Harris (1919). *Striostrea alabamiensis* is actually a synonym of *Striostrea gigantissima* (Finch, 1824) as proposed by Harris (1919) and Lawrence (1995: 193). Harris (1919) thought that Finch's description was not sufficient to be valid. Howe (1937) argued that Finch's description was as informative as those of some of his contemporaries and should be considered valid. Other extinct crassostreine species with a riblet-bearing surficial layer based on the literature include *Ostrea dorsata* Deshayes, 1824 (Deshayes, 1824; J.D.C. Sowerby, 1850; Wood, 1861–1871), *Ostrea spatulata* Lamarck, 1806 (Deshayes, 1824), *Ostrea tenera* J. Sowerby, 1821 (J.D.C. Sowerby, 1850; Wood, 1861–1871), *Ostrea velata* Wood, 1861 (Wood, 1861–1871) and *Crassostrea cahobasensis* (Pilsbry and Brown, 1917) (Woodring, 1982).

Lawrence (1995) argued that all of the crassostreine genera should be included in *Crassostrea*. Part of his argument was based on the presence of chomata on *C. gigantissima* and *C. cahobasensis* and a riblet-bearing surficial layer on *C. gigantissima*. However, since both of these species have chomata and a riblet-bearing surficial layer and since these are currently considered diagnostic characters for the genus *Striostrea*, then at least for *Striostrea* his argument is not valid.

Carter et al. (2011) proposed placing the crassostreine oysters in the family Flemingostreidae Stenzel, 1971. According to Carter et al. (2011), this family contains the extinct paraphyletic subfamilies Flemingostreinae Stenzel, 1971 and Liostreinae Vialov, 1983 and the extant subfamily Crassostreinae Scarlato and Starobogatov, 1979. The living crassostreine oysters were originally placed in their own family (Crassostreidae) by Scarlato and Starobogatov (1979: 46) on the basis: "Non-incubating oysters, because of the presence in them of such morphological structures as a promyal cavity (promyal passage) and peculiarities of reproduction" and "The family is characterized by the development of a promyal cavity, the pericardium shifted before the adductor muscle anteriorly, and to the right, and the union of the anterior part of the suprabranchial cavity with its excurrent part. In the left (attached) valve there is usually a deep subumbonal cavity. The eggs develop internally, the sexes are separate (possibly protandric hermaphrodites, but with a regular and complete sex change phase)." In order to include the Flemingostreinae and Liostreinae in the same family-group rank with the Crassostreinae, the obligate choice for family name was Flemingostreidae (Nikolaus Malchus, personal communication). See synonymy list under the systematics section.

OCCURRENCES, STRATIGRAPHY, AND AGE

Over forty complete valves (some paired) of *Striostrea paucichomata* Bolton new species have been examined in the FLMNH Invertebrate Paleontology Collections. All were derived from the two most densely-packed and species-rich molluscan units of southern Florida; namely the Pinecrest beds of the Tamiami Formation and the Caloosahatchee Formation. The majority was recorded from the Pinecrest beds in northwestern Sarasota County with the remainder collected from Broward, Charlotte, De Soto, and Hendry counties (see Figure 1).

Much confusion and controversy surround surface and near-surface deposits (especially the Tamiami Formation) of southern Florida. As summarized by Jones (1997: 107) this is because "Pliocene and Pleistocene deposits in the region consist of siliciclastic and carbonate lithologies whose lateral and temporal relationships are obscured by 1) thinness and discontinuous distribution of units, 2) limited exposures, 3) rapid facies changes, and 4) repeated advance and retreat of the sea over this low-elevation region in response to the many sea-level oscillations of the Plio-Pleistocene". Additionally, many stratigraphic units have been erected not based on lithology (as now required by the North American Stratigraphic Code) but fossil content (Scott, 1992).

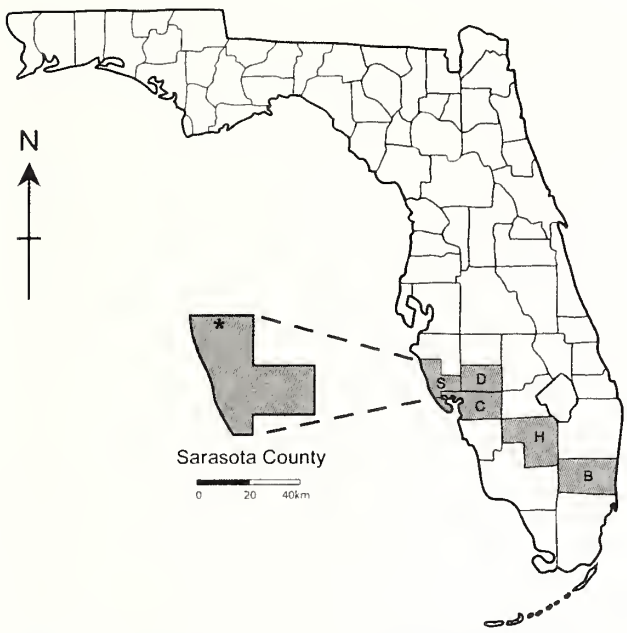


Figure 1. Florida map showing *Striostrea paucichomata* Bolton **new species** type area (depicted by *); equals now defunct APAC Sarasota Mines (formerly Macasphalt Shell Pits, Newburn Road Pit, Warren Brothers Pits) and active SMR Aggregates Pits (formerly Wendell Kent Pit, Richardson Road Shell Pits, Quality Aggregates Shell Pits). All counties – Sarasota (S), De Soto (D), Charlotte (C), Hendry (H) and Broward (B) where occurrences are known are shaded.

Herein, we use widely-accepted stratigraphic terminology for both units (Tamiami and Caloosahatchee formations) in which *S. paucichomata* is known to occur (e.g., Zullo and Harris, 1992). For a more thorough review of southern Florida stratigraphy refer to Lyons (1991).

The name "Tamiami limestone" was first applied by Mansfield (1939) for deposits exposed during road construction in Collier and Monroe counties. Parker and Cooke (1944) broadened the concept of the Tamiami limestone and designated it a formation. They also included the sands near Pinecrest, as described in Mansfield (1931), in their concept and concluded that the Buckingham limestone of Mansfield (1939) was a facies of the Tamiami Formation. Parker (1951) placed the Buckingham limestone in the Tamiami Formation, and Olsson (1964) informally proposed the "Pinecrest beds" for fossil deposits younger than the Tamiami Formation and older than the Caloosahatchee marl. Hunter (1968) divided the Tamiami Formation into five, major, members based on lithostratigraphy; Bayshore Clay, Murdock Station member, Pinecrest sand, Ochopee limestone, and Buckingham limestone. She considered the three youngest members, the Pinecrest sand, Ochopee limestone, and Buckingham limestone, to be lateral equivalents; her oldest member being the Bayshore clay. However, Missimer (1992, p. 63) reported that the Tamiami Formation "consists of at least nine mappable members or facies" including the Pinecrest Sand, Ochopee Limestone and Buckingham Limestone. Due to the poorly defined, lithologically (carbonates, siliciclastics, and mixed siliciclastics-carbonates), and temporally complex nature of the Tamiami Formation, Zullo and Harris (1992) employed sequence stratigraphy to help unravel both its temporal and spatial relationships. For the purposes of this study we follow their nomenclature of this marine deposit, especially in the type area of *S. paucichomata* (Figures 1 and 2).

Today, the Pinecrest beds are best exposed at Schroeder-Manatee Ranch Aggregates, Inc. (SMR) excavations (formerly Richardson Road Shell Pits and Quality Aggregates Shell Pits) in Sarasota County (Figure 1); now that the more westward Ashland Petroleum and Asphalt Corporation (APAC) Sarasota pits (formerly Newburn Road Pit, Warren Brothers Pits, and Macasphalt Shell Pits) are water-filled. At APAC, Petuch (1982) divided the exposed beds into twelve units. Based on the aforementioned sequence stratigraphic analysis of Zullo and Harris (1992) at APAC and SMR, they concluded that Petuch Units 0–1 belong to the Caloosahatchee Formation and Units 2–11 were Tamiami Formation. Units 2–9 were divided into the Upper Tamiami Formation and Units 10–11 were Lower Tamiami Formation. Further subdivision placed Units 2–3 into the upper Pinecrest beds and Units 4–9 into the lower Pinecrest beds (see Figure 2). Herein, we follow the stratigraphic organization proposed Zullo and Harris (1992) although Petuch and Drolshagen (2011) now consider Units 2–4 to belong to the Fruitville Member (Tamiami Formation), Units 5–9 to belong to the Pinecrest Member (Tamiami Formation), Unit 10 to belong to the Buckingham Member (Tamiami Formation), and Unit 11 to be the Sarasota Member (Murdock Station Formation).

Jones et al. (1991) estimated the age of Petuch's (1982) Units 2–4 as being 2.25 (+/– 0.25) Ma and Units 5–10 as being 3.0 (+/– 0.5) Ma based on $^{87}Sr/^{86}Sr$ isotope bivalve dating, paleomagnetism, and invertebrate and vertebrate biochronology. Allmon (1993) concluded that Units 5–10 are upper Pliocene (3.0–3.5 Ma) and Units 2–4 are much younger (2.0–2.5 Ma). Gibbard et al. (2009) places the boundary between the Pliocene and the Pleistocene at 2.588 Ma. Therefore, Units 2–4 with a minimum age of 2.0 Ma and maximum age of 2.5 Ma is lower Pleistocene. Units 5–10 with a minimum age of 2.5 Ma and a maximum age of 3.5 Ma is mostly, if not wholly, upper Pliocene. The underlying Unit 11 is therefore at least upper Pliocene.

The name "Caloosahatchee beds of marls" was applied by Dall (1887) for shell horizons exposed along the Caloosahatchee River. Matson and Clapp (1909) later referred to the unit as "Caloosahatchee marl" and DuBar (1974: 216) elevated it to formational status because "of the diversity of lithologies and the vagueness of the term marls". Today, the southern peninsular Florida marine, brackish, and freshwater units which are younger than the Tamiami Formation and older than the Bermont Formation are placed within this unit (DuBar, 1974).

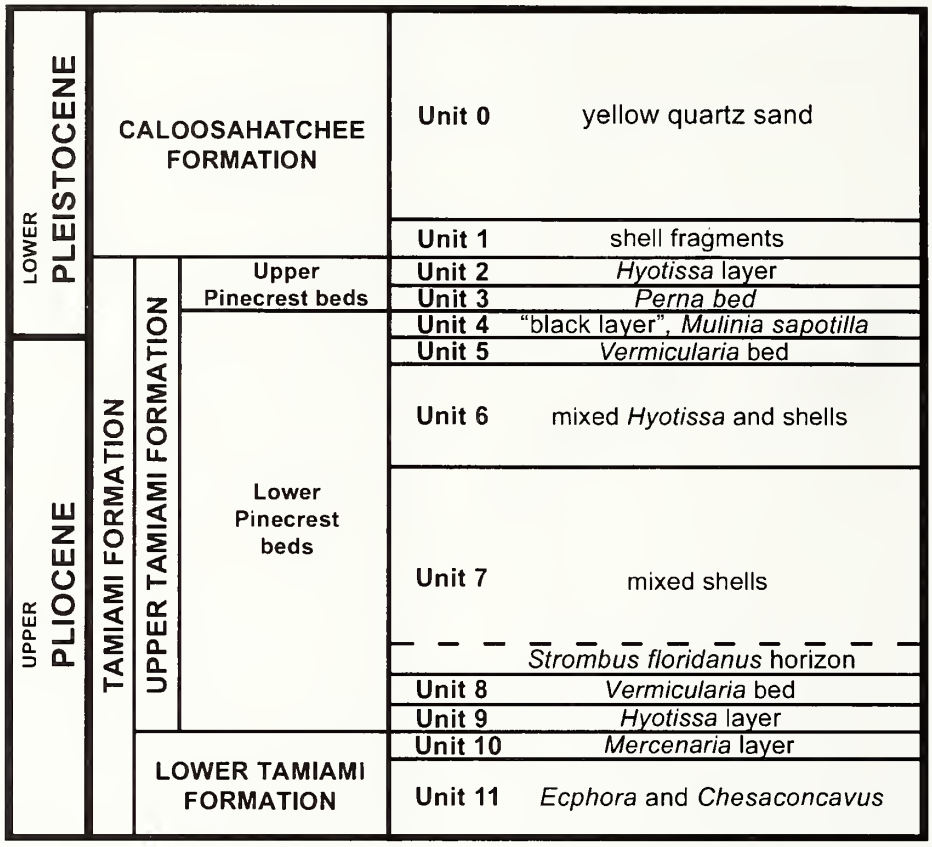


Figure 2. Stratigraphic nomenclature for the type area of *Striostrea paucichomata* Bolton **new species** in Sarasota County modified from Zullo and Harris (1992) and incorporating stratigraphic units of Petuch (1982). The new species has thus far been recorded from Units 3, 5 through 8 and 10.

The Caloosahatchee Formation disconformably overlies the Tamiami Formation and has been estimated to be about 1.8 Ma using He/U coral dating (Muhs et al., 1992). This places the unit in the late lower Pleistocene.

SYSTEMATICS

Class Bivalvia Linnaeus, 1758
Order Ostreida Férussac, 1822 in 1821–1822
Superfamily Ostreoidea Rafinesque, 1815
Family Flemingostreidae Stenzel, 1971
Flemingostreini Stenzel, 1971
Crassostreidae Scarlato and Starobogatov, 1979
Crassostreini Chiplankar and Badve, 1979
Crassostreinae Torigoe, 1981
Crassostreinae Freneix, 1982
Liostreinae Vialov, 1983
Subfamily Crassostreinae Scarlato and Starobogatov, 1979
Tribe Striostreini Harry, 1985

Genus *Striostrea* Vialov, 1936

Type Species: *Ostrea procellosa* Lamy, 1929, which is a junior synonym of *Ostrea margaritacea* Lamarck, 1819. Recent, along the coast of South Africa and the western Indian Ocean as far north as the Arabian Peninsula (Huber, 2010).

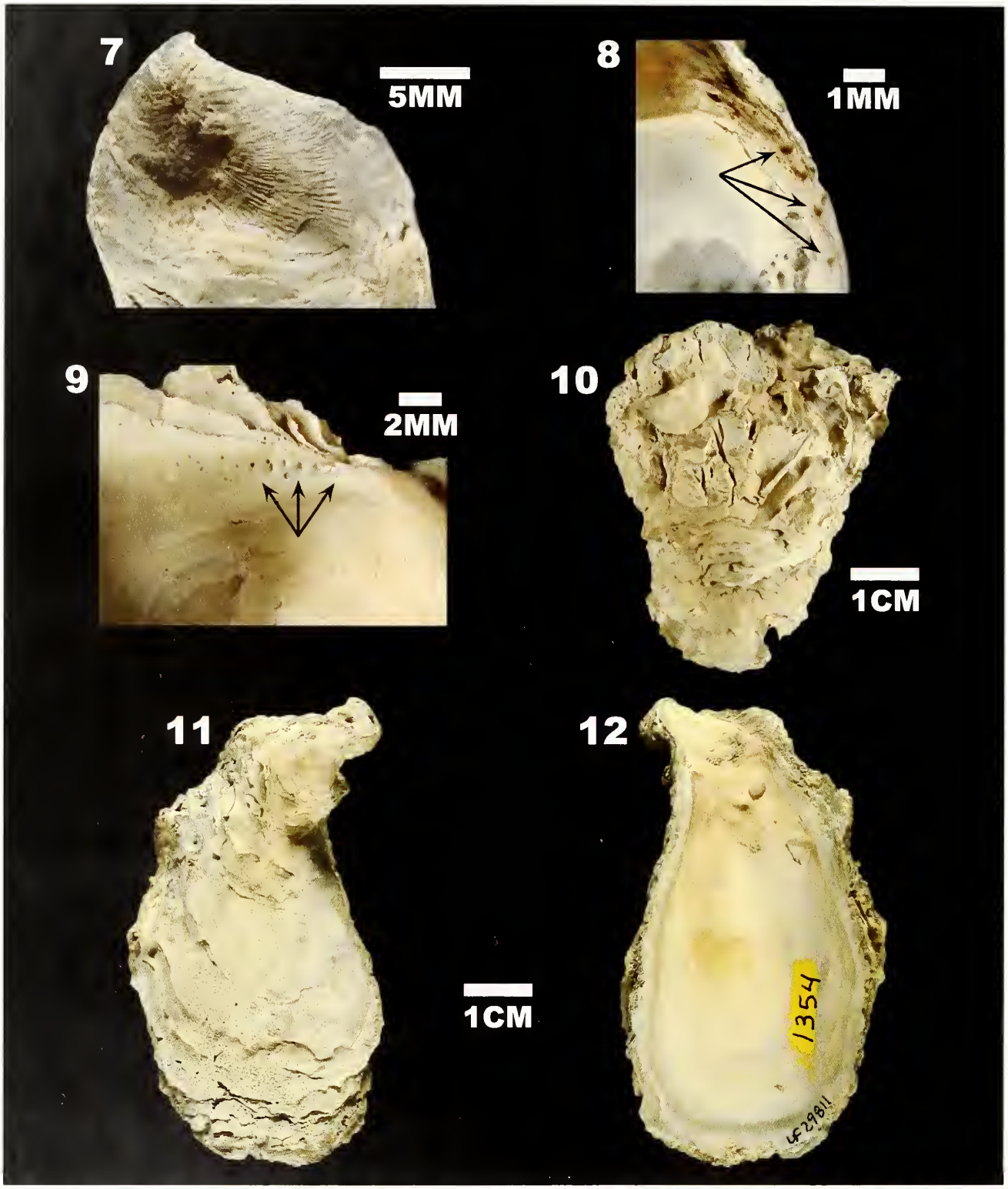
Striostrea paucichomata Bolton new species

(Figures 3–12)

Diagnosis: Right valve with riblet-bearing surficial layer (only visible on exceptionally well-preserved specimens), weakly developed chomata usually present on both valves (not visible in about 30% of specimens), left valve external surface usually with characteristic irregular and undulating growth intervals, maximum height about 8 cm, posterior adductor muscle imprint situated about mid-point between ventral edge of hinge and ventral margin of shell.

Description: Shell usually elongate dorsoventrally (Figures 3–6, 11–12). Holotype maximum dimensions: left valve 6.56 cm high, 3.08 cm long, 1.72 cm wide; right valve 5.58 cm high, 2.33 cm long, 0.2 cm wide. Maximum height about 8 cm. Left valve usually without extensive attachment area; usually moderately to deeply concave; umbonal cavity weakly to strongly developed depending on degree of valve concavity; external surface usually with characteristic irregular and undulating growth intervals (Figure 3). Right valve

Figures 3–6. Paired valves of *Striostrea paucichomata* Bolton new species. Holotype (UF 34779). **3.** Exterior of left valve. **4.** Interior of left valve. **5.** Exterior of right valve. **6.** Interior of right valve.



Figures 7–12. *Striostrea paucichomata* Bolton new species. **7.** Exterior detail of right valve near hinge showing the riblet-bearing surficial layer. Holotype (UF 34779). **8.** Interior detail of right valve near hinge showing anachomata (see arrows). Holotype (UF 34779). **9.** Interior detail of left valve near hinge showing catachomata (see arrows), same specimen as Figure 10. Paratype (UF 200351). **10.** Exterior of left valve showing variation in appearance. Paratype (UF 200351). **11.** Exterior of left valve showing variation in appearance, same specimen as Figure 12. Paratype (UF 29811). **12.** Interior of left valve. Paratype (UF 29811).

usually flat; with regular, closely spaced growth lines (Figure 5); exceptionally well-preserved specimens with riblet-bearing surficial layer consistent with the description in Stenzel (1971: N979, N1136) (Figure 7), may only be present near hinge, riblets 0.1–0.2 mm wide. Both valves usually with weakly developed ostreine chomata (Figures 8–9), not visible in about 30% of specimens, only present near hinge, older specimens usually with relict chomata or chomata absent, anachomata 0.1–0.3 mm wide with 0.1–1.5 mm gap between them, chomata may be difficult to see without magnification. Shell not thick as *S. gigantissima* and *S. cahobasensis* commonly are. Posterior adductor muscle imprint situated about mid-point between ventral edge of hinge and ventral margin of shell (compared to ventral to the mid-point in *Crassostrea virginica*), usually semilunar in outline (Figures 4, 6, 12).

Holotype (Figures 3–8): UF 34779, left and right valves (pair), USA, Florida, Sarasota Co., Macasphalt Shell Pit (SO001), T36S, R18E, Plio-Pleistocene, spoil, 1 Nov. 1986, R.J. Britt, Jr.

Paratypes: UF 200351, two left valves, USA, Florida, Sarasota Co., Quality Aggregates Phase 07 (SO022), T36S, R19E, Pliocene, upper Tamiami Formation, upper Pinecrest beds, Petuch Unit 3?, 7 June 1994, R. Portell et al. (Figures 9–10); UF 216676, one left valve, USA, Florida, Sarasota Co., Macasphalt Shell Pit B (SO017), T36S, R18E, Pliocene, upper Tamiami Formation, lower Pinecrest beds, Petuch Unit 5, 16 March 1988, R. Portell and D. Jones; UF 38987, two left valves, USA, Florida, Sarasota Co., Macasphalt Shell Pit B (SO017), T36S, R18E, Pliocene, upper Tamiami Formation, lower Pinecrest beds, Section 2, Petuch Unit 6, 16 March 1988 R. Portell and D. Kendrick; UF 53225, three left valves, USA, Florida, Sarasota Co., Richardson Road Shell Pit 01B (SO013), T36S, R19E, Pliocene, upper Tamiami Formation, lower Pinecrest beds, Petuch Unit 7, 19 April 1991, R. Portell and D. Jones; UF 178522, two right valves, USA, Florida, Sarasota Co., Quality Aggregates Phase 8 REU-2 (SO049), T36S, R19E, Pliocene, upper Tamiami Formation, lower Pinecrest beds, REU Unit 2A, 3–4 June 2006, USF REU; UF 53629, one right valve, USA, Florida, Sarasota Co., Richardson Road Shell Pit 01B (SO013), T36S, R19E, Pliocene, upper Tamiami Formation, lower Pinecrest beds, Petuch Unit 8, 19 April 1991, R. Portell and D. Jones; UF 95889, one left valve, USA, Florida, Sarasota Co., Richardson Road Shell Pit 01C (SO021), Pliocene, lower Tamiami Formation, Petuch Unit 10, R. Portell and D. Jones; UF 29811, left and right valves (pair), USA, Florida, Sarasota Co., Macasphalt Shell Pit (SO001), T36S, R18E, Plio-Pleistocene, spoil, 1969–1978, E. and E. Bradley (Figures 11–12).

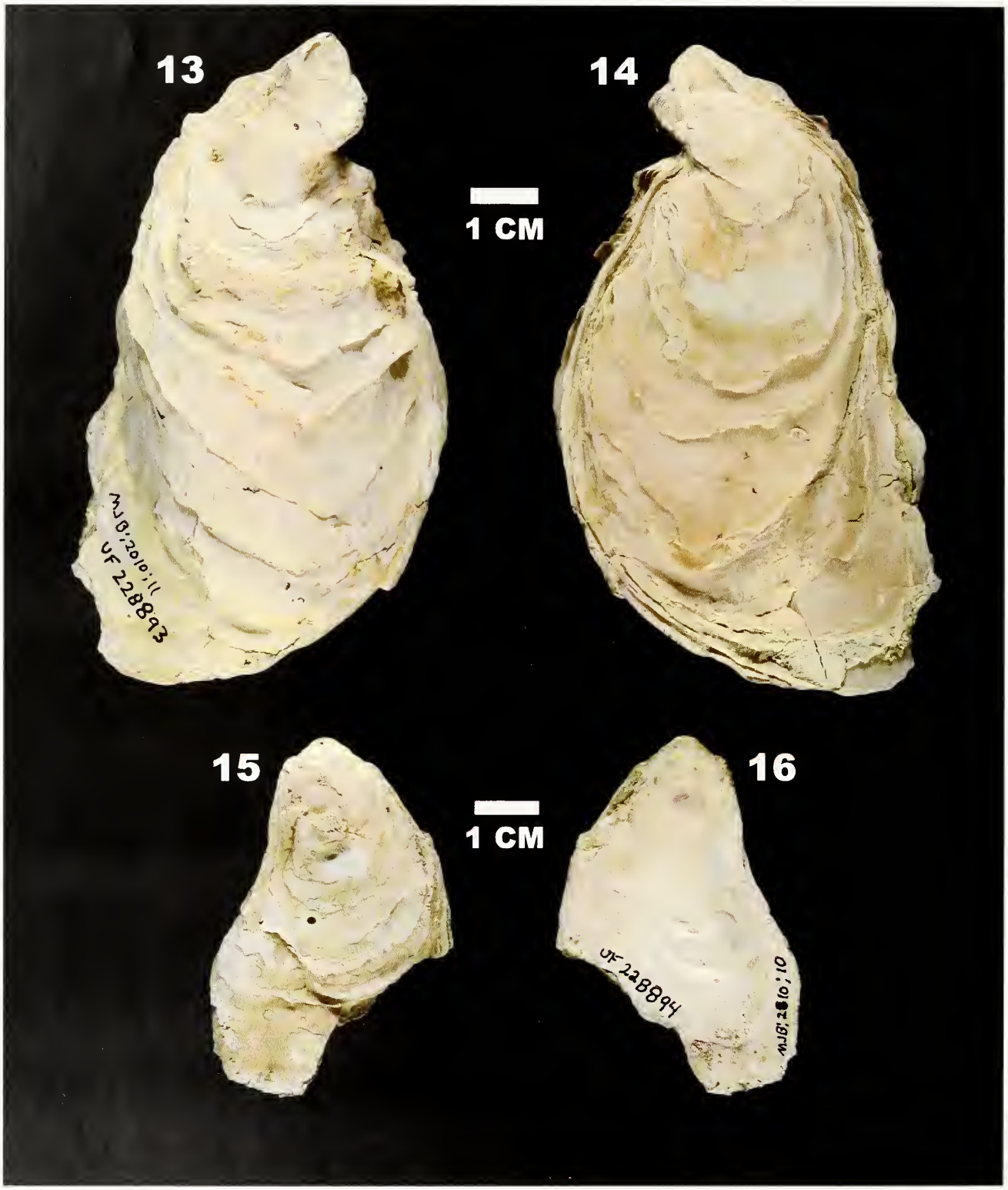
Additional Specimens from Other Locations or Formations: UF 93046, one right valve, USA, Florida, Charlotte Co., Acline Shell Pit (CH010), T41S, R23E, Pliocene, Tamiami Formation, Pinecrest beds, Florida Geological Survey/C.R. Locklin; UF 208478, two left valves, USA, Florida, Hendry Co., Interceptor Canal 01 (HN027), T48S, R34E, Pliocene, Tamiami Formation, Pincrest beds, 1968, H.K. Brooks and D. Townsend; UF 208483, two right valves, USA, Florida, Broward Co., south of Seminole Indian Reservation headquarters, just north of lock on drainage canal (5422), Pliocene, Tamiami Formation, Pinecrest beds, 1969, H.K. Brooks et al.; UF 200355, three left valves and two right valves, USA, Florida, De Soto Co., De Soto Shell Pit 05 (DE010), T39S, R25E, lower Pleistocene, Caloosahatchee Formation, Portell Bed 7, 7 March, 1991, R. Portell and K. Schindler; UF 200354, two right valves, USA, Florida, Hendry Co., Caloosahatchee River 09, T45S, R28E, early Pleistocene, Caloosahatchee Formation, DuBar Horizon 5, 1953, J. DuBar; UF 2654, left and right valves (pair) and one right valve, USA, Florida, Hendry Co., Caloosahatchee River 01 (HN002), T43S, R28/29E, lower Pleistocene, Caloosahatchee Formation, spoil, J.C. Macbeth.

Occurrence: *Striostrea paucichomata* is known from the upper Pliocene to lower Pleistocene Tamiami Formation and lower Pleistocene Caloosahatchee Formation in Sarasota (type area), Charlotte, De Soto, Hendry and Broward counties, Florida (Figure 1). Specimens have been found at the type location in the upper Tamiami Formation, Pinecrest beds in Petuch Units 3, 5, 6, 7, 8 and lower Tamiami Formation Unit 10.

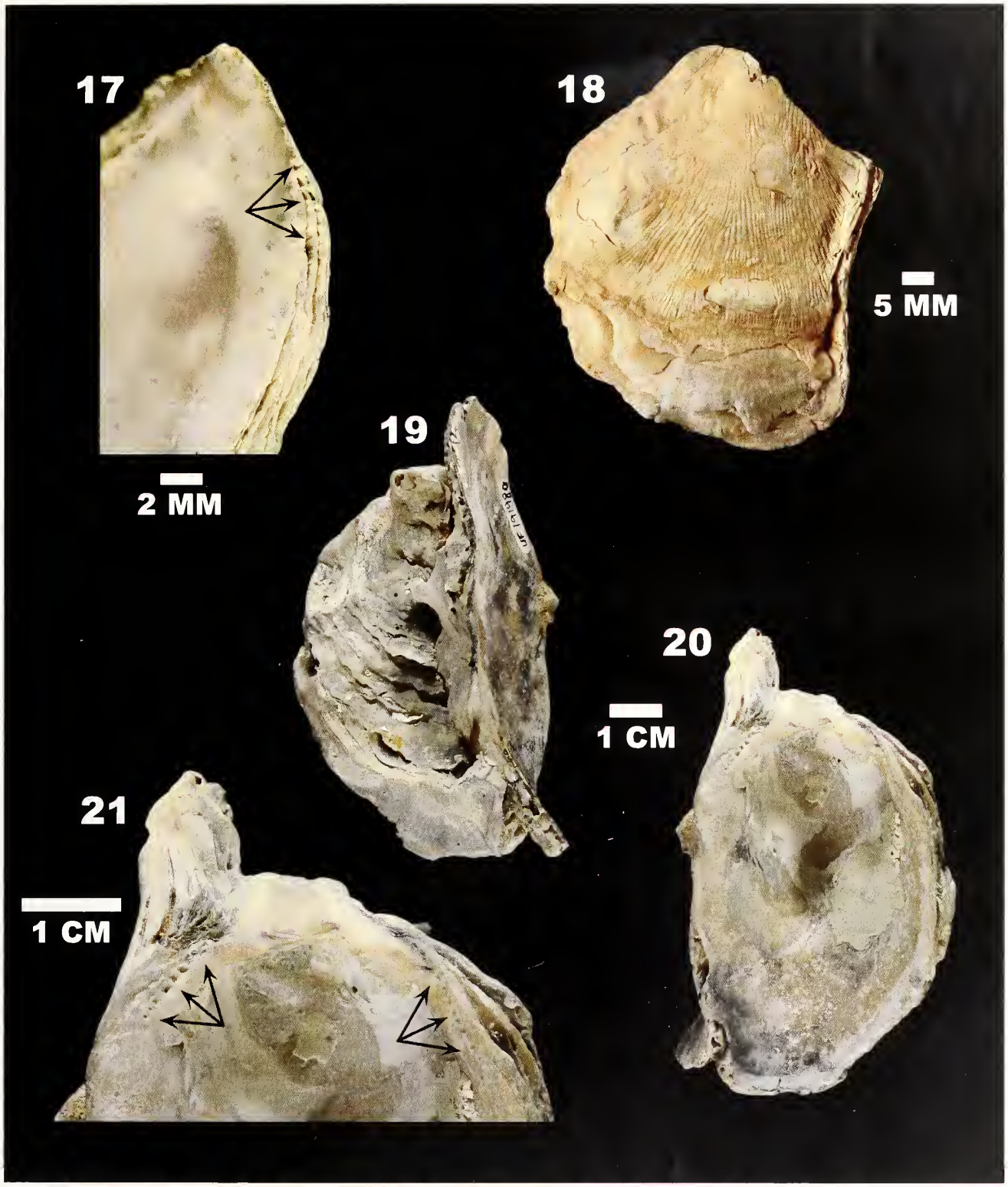
Etymology: The species name is derived from the Latin *pauci* meaning few and "chomata" which are the tubercles and pits on the periphery of inner surface of shells, usually near the hinge. This name is in reference to the usually low number of chomata that are often difficult to see or absent.

Discussion: Identification of fossil oysters has been confused and neglected due to the high amount of morphological variation associated with environmental factors. This condition has led to the publication of many synonyms based on either different ecophenotypes or the differences between young and old specimens (Stenzel, 1963). The proliferation of species names has also been the result of some authors describing new species based on a very limited number of specimens. However, given adequate material and using the characters described in Stenzel (1971) and Harry (1985), accurate generic identifications of most Cenozoic oysters should be possible.

Use of the genus *Striostrea* for crassostreine oysters with a riblet-bearing surficial layer and chomata has not been widely used in North America. This may partially be due to the riblet-bearing layer being fragile and only present on exceptionally well-preserved specimens and the chomata are not visible on all specimens either because they were only present on young specimens or are present as relict or active chomata only on a percentage of older individuals. For *S. paucichomata* these characters are also often difficult to see without



Figures 13–16. *Striostrea gigantissima* (Finch, 1824). **13.** Exterior of left valve, same specimen as Figure 14 (UF 228893). **14.** Exterior of right valve (UF 228893). **15.** Exterior of right valve, same specimen as Figures 16 and 17 (UF 228894). **16.** Interior of right valve (UF 228894).



Figures 17–21. *Striostrea gigantissima* (Finch, 1824) (**17**, **18**). **17.** Interior detail of right valve near hinge showing anachomata (see arrows). (UF 228894). **18.** Exterior of right valve showing the riblet-bearing surficial layer. (UF 228895). *Striostrea cahobasensis* (Pilsbry and Brown, 1917) (**19–21**). **19.** Exterior of left valve, same specimen as Figures 20 and 21 (UF 191980). **20.** Interior of left valve (UF 191980). **21.** Interior detail of left valve near hinge showing catachomata (see arrows). (UF 191980).

magnification. For these reasons, to accurately identify fossil *Striostrea* it is important to have sufficient numbers of exceptionally well-preserved specimens including ones of different age classes.

Fossil *Striostrea* known from the western Atlantic include *S. gigantissima* (Finch) (lower Eocene through upper Oligocene; USA: North Carolina–Texas), *S. cahobasensis* (Pilsbry and Brown) **new combination** (upper Oligocene through middle Miocene; Caribbean: Venezuela, Panama, Puerto Rico, Haiti, Mexico; USA: FL), and *S. paucichomata* Bolton new species (upper Pliocene through lower Pleistocene; USA: FL). Photos of young specimens of *S. gigantissima* (Figures 13–18) from the upper Eocene of Georgia and *S. cahobasensis* from the lower Miocene (Figures 19–21) and upper Oligocene (Figures 22, 23) of Florida are provided for comparison. A key for the Cenozoic crassostreine oysters known from southeastern United States is provided below. There are also specimens of a large crassostreine oyster in the FLMNH Invertebrate Paleontology Collection from the Pliocene of Curaçao (an island off the coast of Venezuela) that may be a *Striostrea*. Young specimens have chomata (UF 114702, UF 116000, UF 116005), but no surface riblets were present on the right valves. However, the specimens were not sufficiently preserved to exhibit a riblet-bearing surficial layer. Furthermore, they very much resemble the eastern Pacific species *Crassostrea titan* (Conrad, 1853) in shape and size. Additional study is required to determine if they are conspecific. The complete temporal and paleogeographic distribution of *Striostrea* will not be known until museum collections are reexamined using the characters and caveats discussed in this paper. Four living species of *Striostrea* are known from the eastern Atlantic Ocean along the coast of tropical West Africa, the coast of South Africa and western Indian Ocean along the coast of East Africa as far north as the Arabian Peninsula, northern Pacific Ocean from Japan to Taiwan, and tropical eastern Pacific Ocean (Huber, 2010).

Key to Cenozoic Crassostreine Oysters Known From the Southeastern United States:

1 Shell without chomata; right valve without a riblet-bearing surficial layer (visible only on exceptionally well-preserved specimens); shell may have costae (primarily on the left valve) and may have plicae along the ventral margin; posterior adductor muscle imprint usually situated ventral to the mid-point between ventral edge of hinge and ventral margin of shell; upper Oligocene – present. ..... ***Crassostrea virginica* (Gmelin, 1791)**

1′ Shell with ostreine chomata (may be absent in older shells and various ecomorphs) (Figures 8, 9, 17, 21, 23); right valve with a riblet-bearing surficial layer (visible only on exceptionally well-preserved

Figures 22–23. *Striostrea cahobasensis* (Pilsbry and Brown, 1917). **22.** Exterior of left valve, same specimen as Figure 23 (UF 27389). **23.** Interior detail of left valve near hinge showing catachomata (see arrows). (UF 27389).

specimens, especially younger ones) (Figures 7, 18); shell usually without costae or plicae. **2**

2(1′) Both valves of similar convexity (especially old shells) or left valve slightly to moderately more convex and capacious; maximum shell height about 56 cm; shell may be extremely thick (see Harris, 1919: Pls. 1–6; Howe, 1937: Pl. 44 Figs. 1–6; Toulmin, 1977: Pl. 14 Figs. 5, 6, Pl. 15 Figs. 1, 2, Pl. 56 Fig. 7); lower Eocene – upper Oligocene. . . . . ***Striostrea gigantissima* (Finch, 1824)**

2′ Left valve usually more convex and capacious than right valve; maximum height less than 20 cm. **3**

3(2′) Chomata moderately developed or absent (Figures 21, 23); shell maximum height about 19.5 cm; shell may be thick (see Pilsbry and Brown, 1917: Pl. 6 Figs. 1, 8; Woodring, 1982: Pl. 90 Fig. 21, Pl. 93 Figs. 6, 7, 9–11, Pl. 94 Figs. 1, 3, 5, Pl. 102 Figs. 1, 5, Pl. 103 Fig. 8, Pl. 106 Figs. 2, 6, 7); upper Oligocene – middle Miocene. . . . . ***Striostrea cahobasensis* (Pilsbry and Brown, 1917)**

3′ Chomata weakly developed or absent (Figures 8, 9); shell maximum height about 8 cm; shell not thick (Figures 3–6, 11–12); upper Pliocene – lower Pleistocene. . . . . ***Striostrea paucichomata* Bolton new species**

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LITERATURE CITED

Allmon, W.D. 1993. Age, environment and mode of deposition of the densely fossiliferous Pinecrest Sand (Pliocene of Florida): Implications for the role of biological productivity in shell bed formation. Palaios 8: 183–201.

Broderip, W.J. 1832. Characters of new species of Mollusca and Conchifera, collected by Mr. Cuming. Proceedings of the Zoological Society of London 2: 25–33.

Campbell, L.D. 1993. Pliocene molluscs from the Yorktown and Chowan River formations in Virginia. Virginia Division of Mineral Resources, Publication 127, 259 pp.

Carter, J.G., C.R. Altaba, L.C. Anderson, R. Araujo, A.S. Biakov, A.E. Bogan, D.C. Campbell, M. Campbell, C. Jin-hua, J.C.W. Cope, G. Delvene, H.H. Dijkstra, F. Zong-jie, R.N. Gardner, V.A. Gavrilova, I.A. Goncharova, P.J. Harries, J.H. Hartman, M. Hautmann, W.R. Hoeh, J. Hylleberg, J. Bao-yu, P. Johnston, L. Kirkendale, K. Kleemann, J. Koppka, J. Kříž, D. Machado, N. Malchus, A. Márquez-Aliaga, J. Masse, C.A. McRoberts, P.U. Middelfart, S. Mitchell, L.A. Nevesskaja, S. Özer, J. Pojeta, Jr., I.V. Polubotko, J.M. Pons, S. Popov, T. Sánchez, A.F. Sartori, R.W. Scott, I.I. Sey, J.H. Signorelli, V.V. Silantiev, P.W. Skelton, T. Steuber, J.B. Waterhouse, G.L. Wingard, and T. Yancey. 2011. A synoptical classification of the Bivalvia (Mollusca). Paleontological Institute, University of Kansas, Paleontological Contributions No. 4, 47 pp.

Chiplonkar, G.W. and R.M. Badve. 1979. Taxonomic comments on subfamily Ostreinae Rafinesque. Proceedings of the Indian Academy of Science B 88: 441–447.

Conrad, T.A. 1840. Fossils of the medial Tertiary of the United States. No. 2. Philadelphia PA., Judah Dobson pp. 33–56, pls. 18–29.

Conrad, T.A. 1852 (published 1853). Notes on shells with descriptions of new species. Proceedings of the Academy of Natural Sciences of Philadelphia 6: 199–200.

Dall, W.H. 1887. Notes on the geology of Florida. American Journal of Science, Series 3, 34: 161–170.

Deshayes, B.P. 1824–1837. Description des coquilles fossils des environs de Paris. Tome Premier. Conchifères. Paris, 392 pp., 65 pls.

DuBar, J.R. 1958. Stratigraphy and paleontology of the late Neogene strata of the Caloosahatchee River area of southern Florida. Florida Geological Survey, Geological Bulletin No. 40, 267 pp.

DuBar, J.R. 1962. Neogene biostratigraphy of the Charlotte Harbor area in southwestern Florida. Florida Geological Survey, Geological Bulletin No. 43, 83 pp.

DuBar, J.R. 1974. Summary of the Neogene stratigraphy of southern Florida. In: R.Q. Oaks and J.R. DuBar (eds.) Post-Miocene Stratigraphy, Central and Southern Atlantic Coastal Plain. Utah State University Press, Logan, Pp. 206–231.

Férussac. 1821–1822. Tableaux systématiques des animaux mollusques. Paris and London. 184 pp.

Finch, J. 1824. Geological essay on the Tertiary formations in America. American Journal of Science 7: 31–43.

Freneix, S. 1982. Disparité microstructurale du test entre *Gryphaeostrea* et *Gyrostrea* (huitres du Crétacé – Miocène). Nouvelle classification des genres. Annales de Paléontologie, 68: 223–240.

Gardner, J. 1945. Three new species from an upper Miocene oyster "reef" in Tampa Bay. The Nautilus 59: 37–41.

Gibbard, P.L., M.J. Head, M.J.C. Walker, and the Subcommission on Quaternary Stratigraphy. 2009. Formal ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. Journal of Quaternary Science 25: 96–102.

Gmelin, J.F. 1791. Caroli a Linné Systema naturae per regna tria naturae. Edition 13. G. E. Beer, Leipzig, 1(6): 3021–3910.

Hanley, S.C.T. 1846. A description of new species of *Ostrea* in the collection of H. Cuming, Esq. Proceedings of the Zoological Society of London, for 1846, pp. 105–107.

Harris, G.D. 1919. Pelecypoda of the St. Maurice and Claiborne stages. Bulletins of American Paleontology 6(31): 1–268.

Harry, H.W. 1985. Synopsis of the supraspecific classification of living oysters (Bivalvia: Gryphaeidae and Ostreidae). The Veliger 28: 121–158.

Howe, H.V. 1937. Large oysters from the gulf coast Tertiary. Journal of Paleontology 11: 355–366.

Huber, M. 2010. Compendium of Bivalves. ConchBooks, Hackenheim, Germany, 901 pp.

Hunter, M.E. 1968. Molluscan guide fossils in late Miocene sediments of southern Florida. Transactions of the Gulf Coast Association of Geological Societies 18: 439–450.

Jones, D.S. 1997. The marine invertebrate fossil record of Florida. In: A.F. Randazzo and D.S. Jones (eds.) The Geology of Florida. University Press of Florida, Gainesville, pp. 89–117.

Jones, D.S., B.J. MacFadden, S.D. Webb, P.A. Mueller, D.A. Hodell, and T.M. Cronin. 1991. Integrated geochronology of a classic Pliocene fossil site in Florida: Linking marine and terrestrial biochronologies. The Journal of Geology 99(5): 637–648.

Lamarck, J.B. 1802–1809. Mémoires sur les fossils des environs de Paris. Annales du Muséum National d'Histoire Naturelle (Paris) Volumes 1–14; reprinted 1978 by the Paleontological Research Institution, Ithaca, New York.

Lamy, E. 1929–1930. Révision des *Ostrea* vivants du Muséum National d'Historire Naturelle de Paris. Journal de Conchyliologie 73: 1–46 (1929); 71–108 (1929); 133–168 (1929); 233–275 (1930).

Lawrence, D.R. 1995. Diagnosis of the genus *Crassostrea* (Bivalvia, Ostreidae). Malacologia, 36: 185–202.

Lea, I. 1833. Contributions to Geology. Philadelphia, 227 pp., 6 pls.

Linnaeus, C. 1758. Systema naturae per regna tria naturae. Edition 10, Volume 1, Holmiae, 823 pp.

Lyons, W.G. 1991. Post-Miocene species of *Latirus* Montfort, 1810 (Mollusca: Fasciolariidae) of southern Florida, with a review of regional marine biostratigraphy. Florida Museum of Natural History Bulletin 35(3): 131–208.

Mansfield, W.C. 1931. Some Tertiary mollusks from southern Florida. Proceedings of the United States National Museum, 79(21): 1–12.

Mansfield, W.C. 1932. Miocene pelecypods of the Choctawatchee Formation of Florida. Florida Geological Survey, Bulletin, 8, 240 pp.

Mansfield, W.C. 1939. Notes on the upper Tertiary and Pleistocene mollusks of peninsular Florida. Florida Geological Survey, Geological Bulletin, No. 18, 75 pp.

Matson, G.C. and F.G. Clapp. 1909. A preliminary report on the geology of Florida. Florida Geological Survey Second Annual Report, pp. 25–173.

Missimer, T.M. 1992. Stratigraphic relationships of sediment facies within the Tamiami Formation of southwestern Florida: Proposed intraformational correlations. In: T. M. Scott and W.D. Allmon (eds.) Plio-Pleistocene stratigraphy and paleontology of southern Florida. Florida Geological Survey Special Publication 36, pp. 63–92.

Muhs, D.R., B.J. Szabo, L. McCartan, P.B. Maat, C.A. Bush, and R.B. Halley. 1992. Uranium-series estimates of corals from Quaternary marine sediments of southern Florida. In: T. M. Scott and W.D. Allmon (eds.) Plio-Pleistocene stratigraphy and paleontology of southern Florida. Florida Geological Survey Special Publication 36, pp. 41–49.

North American Commission on Stratigraphic Nomenclature. 1983. North American Stratigraphic Code. American Association of Petroleum Geologists Bulletin 67(5): 841–875.

Olsson, A.A. 1942. Tertiary and Quaternary fossils from the Burica Peninsula of Panama and Costa Rica. Bulletins of American Paleontology 27: 153–258, pls. 14–25.

Olsson, A.A. 1964. The geology and stratigraphy of south Florida. In: A.A. Olsson and R.E. Petit. Some Neogene Mollusca from Florida and the Carolinas. Bulletins of American Paleontology, 47(217), pp. 511–526.

Olsson, A.A. and A. Harbison. 1953. Pliocene Mollusca of southern Florida with special reference to those from north Saint Petersburg. The Academy of Natural Sciences of Philadelphia, Monograph 8, 455 pp., 65 pls.

Parker, G.G. 1951. Geologic and hydrologic factors in the perennial yield of the Biscayne aquifer. American Water Works Association Journal 43: 817–834.

Parker, G.G. and C.W. Cooke. 1944. Late Cenozoic geology of southern Florida, with a discussion of the ground water. Florida Geological Survey Bulletin 27, 119 pp.

Petuch, E.J. 1982. Notes on the molluscan paleoecology of the Pinecrest Beds at Sarasota, Florida with the description of *Pyruella*, a stratigraphically important new genus (Gastropoda: Melongenidae). Proceedings of the Academy of Natural Sciences of Philadelphia 134: 12–30.

Petuch, E.J. and M. Drolshagen. 2011. Compendium of Florida Fossil Shells, Volume 1, Middle Miocene to Late Pleistocene Marine Gastropods of the Everglades and Adjacent Areas: Families Strombidae, Cypraeidae, Ovulidae, Eocypraeidae, Triviidae, Conidae, and Conilithidae. MdM Publishing, Wellington, Florida, 412 pp.

Pilsbry, H.A. and A.P. Brown. 1917. Oligocene fossils from the neighborhood of Cartegena, Colombia, with notes on some Haitian species. Proceedings of the Academy of Natural Sciences of Philadelphia, 69: 32–41, pls 5–6.

Rafinesque, C.S. 1815. Analyse de la nature ou tableau de l'univers et des corps organisés. Jean Barravecchia, Palermo, 224 pp.

Rochebrune, A.-T. de. 1895. Diagnoses de mollusques nouveaux, provenant du voyage de M. Diguet en Basse-Californie. Bulletin du Muséum National d'Histoire Naturelle, Paris, 1: 239–243.

Say, T. 1824. An account of some of the fossil shells of Maryland. Journal of the Academy of Natural Sciences of Philadelphia, 4: 124–155, pls. 7–13.

Scarlato, O.A. and Ya.I. Starobogatov. 1979. General evolutionary pattern and the system of the Class Bivalvia. Pp. 5–38 in: Morphology, systematic and phylogeny of mollusks. Transactions of the Zoological Institute, Academy of Sciences, USSR Volume 80 (in Russian). Translated by: K.J. Boss and M.K. Jacobson. 1985. Harvard University, Museum of Comparative Zoology, Department of Mollusks, Special Occasional Publication, No. 5, 67 pp.

Scott, T. 1992. Coastal plains stratigraphy: The dichotomy of biostratigraphy and lithostratigraphy – a philosophical approach to an old problem. In: T.M. Scott and W.D. Allmon (eds.), Plio-Pleistocene stratigraphy and paleontology of southern Florida. Florida Geological Survey Special Publication 36, pp. 21–25.

Sowerby I, G.B., 1850. Descriptions of new species of fossils found by J.S. Heniker, Esq. Pp. 44–53 and plates 9–10, in: J.C. Moore. On some Tertiary beds in the island of San Domingo: from notes by J.S. Heniker, Esq., with remarks on the fossils. The Quarterly Journal of the Geological Society of London 6: 39–53, pls. 9–10.

Sowerby, J. 1821. The mineral conchology of Great Britain. Volume 3. W. Arding, London, 194 pp.

Sowerby, J.D.C. 1850. Notes and descriptions of new species. Pp. 162–194, in: F. Dixon, The geology and fossils of the Tertiary and Cretaceous formations of Sussex. London.

Stanley, S.M. 1986. Anatomy of a regional mass extinction: Plio-Pleistocene decimation of the western Atlantic bivalve fauna. Palaios 1: 17–36.

Stenzel, H.B. 1963. A generic character, can it be lacking in individuals of the species in a given genus? Systematic Zoology 12: 118–121.

Stenzel, H.B. 1971. Oysters, in Moore, R.C., ed., Treatise on Invertebrate Paleontology, part N, volume 3, Mollusca 6, Bivalvia. The Geological Society of America and University of Kansas, pp. N952–N1224.

Torigoe, K. 1981. Oysters in Japan. Journal of Science of the Hiroshima University, Series B, Division 1 (Zoology) 29: 291–419.

Toulmin, L.D. 1977. Stratigraphic distribution of Paleocene and Eocene fossils in the eastern gulf coast region. Geological Survey of Alabama, Monograph 13, Volume I, 602 pp.

Vialov, O.S. 1936. Sur la classification des huîtres. Comptes Rendus (Doklady) de l'Academie des Sciences de l'URSS, Nouvelle Serie, 4(13): 17–20.

Vialov, O.S. 1983. Zagal'na klasifikatsii ustrits [General classification of oysters]. Dopovidi Akademiyi Nauk Ukrayins'koyi RSR (series B), Heolohichni, Khimichni ta Biolohichni Nauky [Doklady Akademii Nauk Ukrainskoi SSR] (series B) 11: 6–8 (in Ukrainian with English and Russian summaries).

Ward, L.W. 1992. Molluscan biostratigraphy of the Miocene, middle Atlantic coastal plain of North America. Virginia Museum of Natural History, Memoir No. 2, 159 pp. and 26 plates.

Ward, L.W. and B.W. Blackwelder. 1987. Late Pliocene and early Pleistocene Mollusca from the James City and Chowan River formations at the Lee Creek Mine. In: Ray, C.E. (ed.). Geology and paleontology of the Lee Creek Mine, North Carolina, II. Smithsonian Contributions to Paleobiology, No. 61, pp. 113–283.

Wood, S.V. 1861–1871. A monograph of the Eocene bivalves of England. Volume 1. Palaeontographical Society, 182 pp., 25 pls.

Woodring, W.P. 1982. Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (pelecypods: Propeamussiidae to Cuspidariidae; additions to families covered in P 306-E; additions to gastropods; cephalopods). United States Geological Survey, Professional Paper, 306-F, pp. 541–759 and 124 plates.

Zullo, V.A. and W.B. Harris. 1992. Sequence stratigraphy of marine Pliocene and lower Pleistocene deposits in southwestern Florida: Preliminary assessment. In: T.M. Scott and W.D. Allmon (eds.), Plio-Pleistocene stratigraphy and paleontology of southern Florida. Florida Geological Survey Special Publication 36, pp. 27–40.

Rediscovery of *Choanopoma*? *smithianum* Pfeiffer, 1866 (Annulariidae) from Haiti and designation of a neotype, with the description of two new species of *Weinlandipoma* Bartsch, 1946

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ABSTRACT

Choanopoma ? *smithianum* Pfeiffer, 1866, was described from "monte Platon" on the western end of the Tiburon Peninsula of Haiti. The species has never been figured and the type specimens are apparently lost. Surveys of the region in 1984 and 2006 rediscovered this "lost" species, which is here allocated to *Weinlandipoma* Bartsch, 1946. A neotype is designated based on this material, the species is redescribed, and compared with similar taxa. Two additional species are described as new, *Weinlandipoma auduboni* and *Weinlandipoma macayaense*.

Additional Keywords: Gastropoda, Annulariidae, Hispaniola, *Weinlandipoma*, new species

INTRODUCTION

Ludwig Pfeiffer often described species without immediate illustration although some taxa might subsequently be figured by him or others. In 1866 Pfeiffer described *Choanopoma* ? *smithianum* from "*in monte Platon insulae Haiti.*" He questioned whether his species belonged in *Choanopoma* because none of his five specimens retained an operculum, a diagnostic characteristic of the genus. The species was never figured. Although the species was mentioned again by Pfeiffer (1876) and listed by Tryon (1867), Kobelt (1880), and Crosse (1891), no additional information was given. Bartsch, in his 1946 review of the Hispaniolan annulariids, uncharacteristically overlooked this name. Watters (2006), based on the facts that the type could not be located at The Natural History Museum (UK) or the Berlin Museum für Naturkunde, where much of Pfeiffer's material that had not been destroyed during World War II resided, and that it had never been illustrated, suggested that the taxon was a *nomen dubium*. But investigation of the type locality (Grego and Šteffek, 2007) revealed a species that undoubtedly represents Pfeiffer's lost *Choanopoma*? *smithianum* as well as previously unrecognized taxa.

Pfeiffer's type locality of "*in monte Platon insulae Haiti*" was stated to be "30 engl. Meilen nordöstlich von Aux-Cayes." This measurement is based on road miles, not straight distance. This site is identifiable as the area of the well-known Citadelle de Platons, on "*monte Platon*" located on the Plain of Formón south of Pic Macaya (the second highest mountain in Haiti at 2,347 m) and Pic Formón (2,219 m). It is reasonable to assume that the original collector had visited the area to view this impressive fortress. Citadelle de Platons was used during the Haitian Revolution (1791–1804) to guard against Napoleon's expeditionary force led by Charles Leclerc to recapture the French colony and reinstate slavery. There is also an adjacent village of Les Platons. Collections at Citadelle de Platons and 27 other neighboring sites near Morne Cavalier, Cay Derniere Jeudi, and the Pic Ouasac ridge revealed only four annulariid species: *Weinlandipoma gonavense* (Weinland, 1880), and three additional species of *Weinlandipoma*. Pfeiffer's brief description could only apply to one of the four species encountered based on circumstantial evidence presented here. We believe that the four *Weinlandipoma* taxa near and at the type locality are *Weinlandipoma smithianum*, *Weinlandipoma gonavense*, *Weinlandipoma auduboni*, new species, and *Weinlandipoma macayaense*, new species.

Clench (1935) collected in the general area but reported only on the Urocoptidae. Thompson (1986) collected extensively in the (then proposed) Parc National Pic Macaya. This material is at the Florida Museum of Natural History (UF) and is included in this study. The collections by Grego and Šteffek at thirteen sites and the collections by Thompson at eleven sites resulted in 1,558 specimens of four *Weinlandipoma* species. Some of these sites were figured and discussed in more detail in Grego and Šteffek (2007).

[1] Posthumously

MATERIALS AND METHODS

Unless noted otherwise, all sites are in the Department du Sud, Haiti. Table 1 lists the material examined and the collections sites. Descriptions and measurements were based on shells oriented with the spire up and the aperture facing the viewer. Minimum and maximum dimensions were based on all adult specimens available. Abbreviations used in text are: BMSM, The Bailey-Matthews Shell Museum, Sanibel, Florida, USA; GTW, Collection of G.T. Watters, USA; Grego coll., Jozef Grego Collection, Slovak Republic; NHMUK, The Natural History Museum, London, UK; OSUM, Ohio State University Museum of Biological Diversity, Columbus, USA; UF, Florida Museum of Natural History, Gainesville, USA.

SYSTEMATICS

Family Annulariidae Henderson and Bartsch, 1920
Subfamily Annulariinae Henderson and Bartsch, 1920

Genus ***Weinlandipoma* Bartsch, 1946**

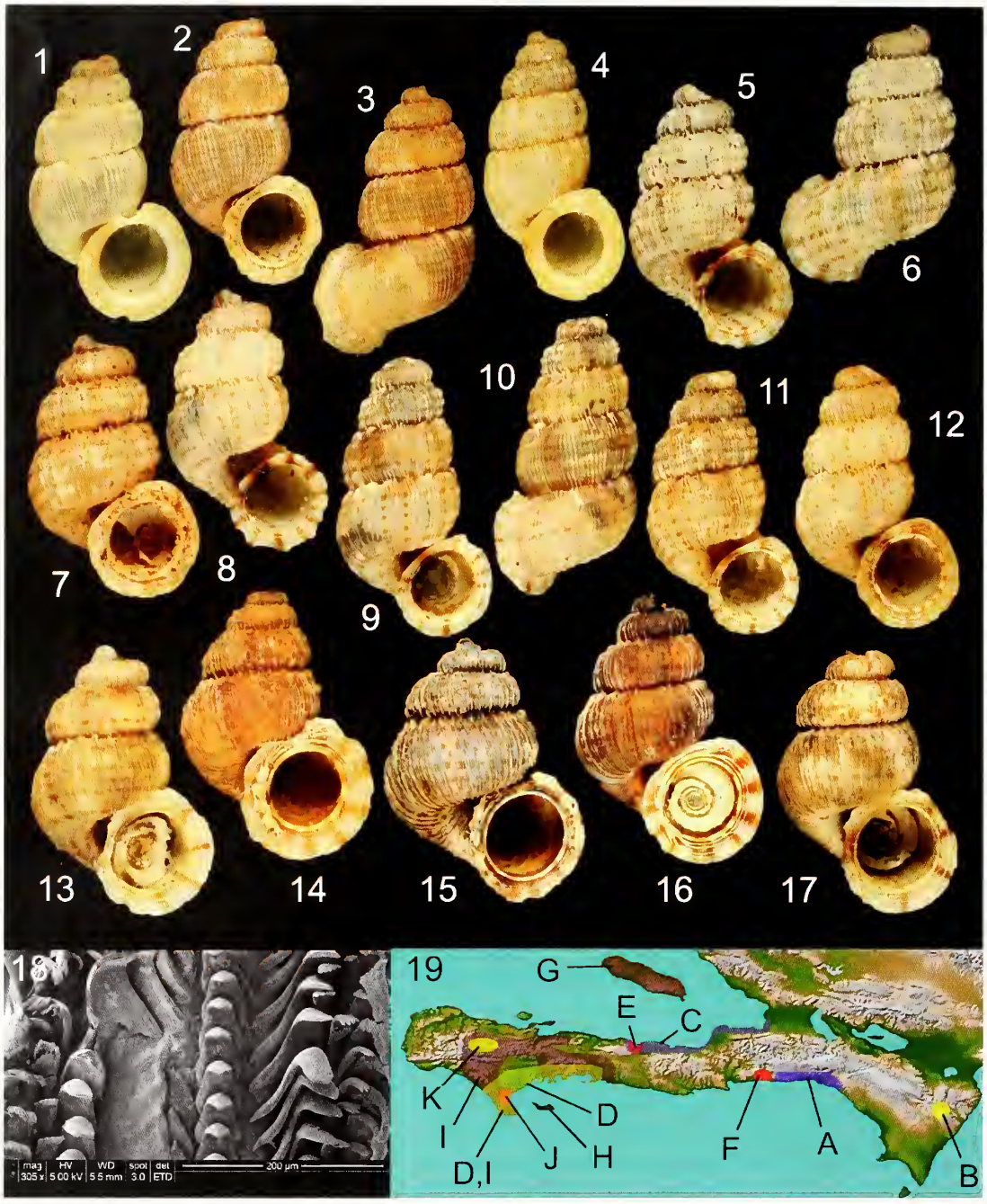
Type Species: *Choanopoma blandii* Weinland, 1880, by original designation.

***Weinlandipoma smithianum* (Pfeiffer, 1866)**
(Figures 1–4, 18)

Choanopoma ? Smithianum Pfeiffer, 1866: 88–89; Pfeiffer, 1876: 157; Watters, 2006: 484, 557 [as a *nomen dubium*].
Choanopoma smithiana Pfeiffer, 1866. Tryon, 1867: 99.

Table 1. Localities and specimens. **A**, *Weinlandipoma audubon*i; **G**, *W. gonavense*; **M**, *W. macayaense*; **S**, *W. smithianum*.

Locality	A	G	M	S
Grego coll., Citadelle de Platons, cleared area around fortress, 727 m elevation, 18.2702° N, −73.9709° W.	1	4	1	3
Grego coll., near Morne Cavalier, sinkholes in wet limestone forest, 1,116 m elevation, 18.3227° N, −74.0204° W	3	102	10	0
Grego coll., near Morn Cavalier, Parc National Pic Macaya, foot of Mt. Ouasac, wet limestone outcrops in cleared forest, 1,341 m elevation, 18.3391° N, −74.0304° W	4	60	5	0
Grego coll., Pic Formón, Parc National Pic Macaya, limestone boulders in cleared wet limestone forest, 1,200 m elevation [coordinates unknown]	0	351	0	0
Grego coll., Cay Derniere Jeudi, Parc National Pic Macaya, wet limestone outcrops at edge of forest, 1,306 m elevation, 18.3397° N, −74.0210° W	0	366	0	0
Grego coll., Cay Derniere Jeudi, Parc National Pic Macaya, wet limestone outcrops at edge of forest, 1,331 m elevation, 18.3397° N, −74.0210° W	0	114	0	0
Grego coll., near Morne Cavalier, 1 km W of Cay Michel, Parc National Pic Macaya, wet limestone outcrops, 1,191 m elevation, 18.3267° N, −74.0297° W	2	20	6	0
Grego coll., Pic Formón, off path between Morne Cavalier and Cay Michel, Parc National Pic Macaya, wet limestone outcrops, 1,202 m elevation, 18.3254° N, −74.0262° W.	0	17	9	32
Grego coll., Pic Ouasac, deforested pine slope, Parc National Pic Macaya, 2,122 m elevation, 18.3576° N, −74.0279° W	0	73	0	0
Grego coll., near Morne Cavalier, 2 km W of Cay Michel, Parc National Pic Macaya, wet limestone outcrops, 1,258 m elevation, 18.3267° N, −74.0297° W	0	20	0	0
Grego coll., Pic Ouasac, Parc National Pic Macaya, deforested pine slope, 1,818 m elevation, 18.3519° N, −74.0282° W	14	33	0	1
Grego coll., Pic Ouasac, Parc National Pic Macaya, deforested pine slope, 1,818 m elevation, 18.3519° N, −74.0282° W	0	77	0	0
Grego coll., Pic Formón, Parc National Pic Macaya, around cave 700 m W of school, cleared wet limestone forest, 1,020 m elevation, 18.3247° N, −74.0130° W	0	21	0	0
UF 77446, 77448, 77453, Morne Formond, Parc National Pic Macaya, 1,650 m elevation, ca. 18.3525° N, −74.0229° W	0	26	0	0
UF 32226, 6 km E of Cavaillon, 200 m elevation, 18.3035° N, −73.6013° W	0	23	0	0
UF 32278, Camp Perrin, 200 m elevation, 18.3274° N, −73.8602° W	0	9	0	0
UF 32269, 1 km S of Camp Perrin, 200 m elevation, 18.3171° N, −73.8601° W	0	38	0	53
UF 32732, Trou Woch Sa Wo, ca. 1 km SSW of Camp Perrin, 18.3188° N, −73.8553° W	0	8	0	0
UF 32323, 7 km NW of Port Salut, 18.1433° N, −73.9647° W	0	7	0	0
UF 32385, 10 km NW of Port Salut, 18.1663° N, −73.9797° W	0	5	0	0
UF 33265, 6 km SSE of Fond des Blancs, 210 m elevation, 18.2341° N, −73.0984° W	0	30	0	0
UF 33375, 3 km E of La Vallée, Nippes Department, ca. 18.4333° N, −73.4346° W	0	6	0	0
UF 32361, 1 km SE of Roche- à-Bateau, 18.1785° N, −73.9913° W	0	3	0	0
UF 48134 – Plaine Sa Wo, [not located, presumably near Trou Woch Sa Wo, ca. 1 km SSW of Camp Perrin, 18.3188° N, −73.8553° W.]	0	0	0	1
Totals	24	1413	31	90



Figures 1–19. *Weinlandipoma* and their distribution. **1–4.** *Weinlandipoma smithianum* (Pfeiffer, 1866). All from Citadelle de Platons. **1.** Grego coll., 9.5 mm length; **2–3.** Neotype of *Choanopoma smithianum* Pfeiffer, 1866. NHMUK 20120258, 9.6 mm length; **4.** Grego coll., 10.6 mm length. **5–8.** *Weinlandipoma auduboni* new species. **5–6.** Holotype UF 451538, near Morne Cavalier, 1 km W of Cay Michel, 7.6 mm length. **7.** Paratype OSUM 37268, Citadelle de Platons, 6.8 mm length; **8.** Paratype BMSM 17935, near Morne Cavalier, 1 km W of Cay Michel, 7.2mm length. **9–12.** *Weinlandipoma macayaense* new species. **9–10.** Holotype UF 451540, near Morne Cavalier, 1 km W of Cay Michel, 9.1 mm length; **11.** Paratype OSUM 37269, Citadelle de Platons. 9.0 mm length; **12.** Paratype BMSM 17936, near Morne Cavalier, 1 km W of Cay Michel, 7.4 mm length. **13–17.** *Weinlandipoma gonavense* Bartsch, 1946. **13.** Grego coll., Mt. Formón, 8.7 mm length. **14.** Grego coll., Citadelle de Platons. 10.6 mm length; **15.** Grego coll. Mt. Formón. 9.9 mm length. **16.** Grego coll. Mt. Formón, 8.9 mm length. **17.** Grego coll., Mt. Ouasac, 17 mm length. **18.** Radula of *Weinlandipoma smithianum* (Pfeiffer, 1866), UF 48134, Plaine Sa Wo. **19.** Distribution of *Weinlandipoma*. Areas are approximations. **A** – *W. meridianum* Bartsch, 1946. **B** – *W. milleri* Bartsch, 1946. **C** – *W. blandii* (Weinland, 1880). **D** – *W. orcuttii* Bartsch, 1946. **E** – *W. strictecostatum* (Maltzan, 1888). **F** – *W. excisum* Bartsch, 1946. **G** – *W. gonavense gonavense* (Weinland, 1880). **H** – *W. gonavense* ssp. of Bartsch, 1946. **I** – *W. gonavense conceptum* Bartsch, 1946. **J** – *W. gonavense robustum* Barstch, 1946. **K** – *W. smithianum* (Pfeiffer, 1866), *W. macayaense* new species, *W. auduboni* new species. Base map courtesy of NASA.

Choanopoma smithianum Pfeiffer, 1866. Kobelt, 1880: 277; Crosse, 1891: 165.

Redescription: Shell small (neotype 9.6 mm length, decollate × 5.8 mm maximum width including peristome), elongate conic. Protoconch unknown, decollate in adults. Teleoconch of 4–4.25 whorls. Axial sculpture of weakly scalloped or undulating cords, regularly spaced, 65–75 on final whorl, more widely spaced on early whorls. On final and penultimate whorls these are grouped in bundles of 4–5 cords where first cord is barely discernable and then each subsequent one increases in size until last cord is longest, then series begins again; this results in an smoothly undulating sutural line. Sculpture is more randomly spaced on earlier whorls. Primary spiral sculpture present only as very weakly scalloped margins of axial cords on earliest whorls and in umbilicus resulting in an angular aspect to base. Secondary spiral sculpture of numerous, microscopic threads between axial cords, often worn away. Suture strongly indented. Aperture double (rarely single), circular (3.5 mm in maximum width in neotype), barely adnate. Inner lip smooth, erect. Outer lip broadly expanded, slightly narrower facing umbilicus, consisting of numerous fused lamella, slightly auriculate. Shell dirty white to pale lavender with 7–8 spiral rows of brown spots and dashes; spots do not continue as bands over lip. Operculum multispiral with a slightly oblique, erect calcareous lamella. Radula taenioglossate with digitate first marginal (Figure 18).

Neotype: NHMUK 20120258 (Figures 2, 3).

Type Locality: The neotype is from the type locality "*in monte Platon insulae Haiti*," here interpreted as Citadelle de Platons, specifically the cleared area around the fortress, 727 m elevation, Department du Sud, Haiti, 18.2702° N, −73.9709° W.

Distribution: Specimens are only known from the type locality, Pic Formón, and near Camp Perrin (UF 32254, 48134). It probably has a narrow range in the southern foothills of the Pic Macaya range of the Massif de la Hotte.

Variation in specimens: Ninety specimens seen. The degree of color pattern intensity varies from dark to barely discernible.

Comparison with Other Species: *Weinlandipoma smithianum*, *W. macayaense*, and *W. auduboni* are most similar to each other and to *W. orcuttii* Bartsch, 1946, described from a hill north of Coteaux. That species is distributed along the southwestern edge of the Tiburon Peninsula from Coteaux to as far east as Aquin. It appears to be a coastal, lowland species whereas *W. smithianum*, *W. macayaense*, and *W. auduboni* are montane. *Weinlandipoma orcuttii* differs from *W. smithianum*, *W. macayaense*, and *W. auduboni* in sculptural differences. In *W. orcuttii* the axial ribs produce swollen sutural cusps of a uniform length resulting in a regular, even row of denticles lining the suture. In *W. smithianum*, *W. macayaense*, and *W. auduboni* these ribs are not of uniform length and are gathered in bundles forming an undulating or ragged row of denticles at the suture. *Weinlandipoma smithianum*, *W. macayaense*, and *W. auduboni* also bear a striking resemblance to *Articulipoma fluxum* (Bartsch, 1946), a species Bartsch described as "exceedingly puzzling" (p. 48). It extends across most of the Tiburon Peninsula from Port-au-Prince to Les Cayes but has not been found in the Citadelle de Platons area. It differs from *Weinlandipoma* in having a paucispiral, flat, chondroid operculum rather than a multispiral operculum with an erect lamella and in lacking microscopic spiral threads between the axial sculpture. However, the overall shell sculpture is very similar.

Weinlandipoma smithianum differs from *W. auduboni* and *W. macayaense* in being larger with much weaker scalloped axial sculpture, a peculiar pattern of sutural sculpture, and a barely adnate aperture.

***Weinlandipoma auduboni* new species**
(Figures 5–8)

Description: Shell small (holotype 7.6 mm length, decollate × 4.4 mm maximum width including peristome), short conic. Protoconch lost in all examples. Teleoconch of 3.75 whorls. Axial sculpture of undulating and strongly scalloped, narrow, erect lamella, 60–70 on final whorl, more widely spaced on early whorls. These are often grouped in bundles of 2–3 lamella into unfused cusps at suture, separated by a wide space containing 1–3 very fine threads that do not form cusps, but this pattern is not consistent on entire shell; this results in a ragged sutural line. Sculpture is more widely spaced on earlier whorls. Primary spiral sculpture present only as strongly scalloped margins of axial lamella; three scallops on spire whorls, seven on final whorl, three of these are prominent in umbilicus. Secondary spiral sculpture of numerous, microscopic threads between axial lamella, often worn away. Suture strongly indented. Aperture double, circular (2.7 mm in maximum width in holotype), always solute. Inner lip smooth, slightly erect. Outer lip expanded, narrower facing umbilicus, consisting of fine, fused lamella, slightly auriculate. Shell dirty white with 6–7 spiral rows of widely separated, small, brown spots and dashes axially aligned; spots continue as bands over both sides of lip and form spots on inner lip. Operculum multispiral with a vertical, erect calcareous lamella.

Holotype: UF 451538.

Type locality: Near Morne Cavalier, 1 km W of Cay Michel, Parc National Pic Macaya, wet limestone outcrops, 1,191 m elevation, Department du Sud, Haiti, 18.3267° N, −74.0299° W.

Paratypes: UF 451541, near Morne Cavalier, foot of Mount Ouasac 1,341 m elevation, Department du Sud, Haiti, 18.3391° N, −74.0304° W (1 specimen); OSUM 37268, Citadelle de Platons, cleared area around fortress, 727 m elevation, Department du Sud, Haiti, 18.2702° N,

−73.9709° W (1 specimen); BMSM 17935, near Morne Cavalier, 1 km W of Cay Michel, Parc National Pic Macaya, wet limestone outcrops, 1,191 m elevation, Department du Sud, Haiti, 18.3267° N, −74.0297° W (1 specimen).

Other Material Examined: Grego coll., Pic Ouasac, Parc National Pic Macaya, deforested pine slope, 1,818 m elevation, 18.3519° N, −74.0282° W (14 specimens); Grego coll., near Morne Cavalier, sinkholes in wet limestone forest, 1,116 m elevation, 18.3227° N, −74.0204° W. (3 specimens); Grego coll., near Morn Cavalier, foot of Mt. Ouasac, wet limestone outcrops in cleared forest, 1,341 m elevation, 18.3391° N, −74.0304° W (3 specimens).

Distribution: Known from Morn Cavalier and Citadelle de Platons between 727–1,818 m elevation; it probably occurs throughout the middle elevations of the Pic Macaya range.

Variation in Specimens: Twenty-four specimens seen. The examples we have seen are very uniform in their characteristics, differing only in the number of axial lamella (60–70).

Comparison with Other Species. *Weinlandipoma audubonì* differs from *W. macayaense* in being smaller (6.2–7.2 mm decollate length vs. 7.2–9.6 mm for *W. macayaense*), in having coarser sculpture, and in having fewer axial lamella (60–70 vs. 70–90 for *W. macayaense*).

Etymology: Named for John James Audubon (1785–1851), ornithologist, naturalist, and painter who was born at nearby Les Cayes, and for the Société Audubon d'Haiti, without whose assistance these collections could not have been made.

***Weinlandipoma macayaense* new species**
(Figures 9–12)

Description: Shell small (holotype 9.1 mm length, decollate × 5.4 mm maximum width including peristome), elongate conic. Protoconch of 1.75 smooth, prominent whorls, usually decollate in adults. Teleoconch of 3.75–4 whorls. Axial sculpture of scalloped lamella, 70–90 on final whorl, more widely spaced on early whorls. On final and penultimate whorls these are grouped in bundles of 3–5 cords with wide species between bundles having 1–5 fine threads. Sculpture is more randomly spaced on earlier whorls. Primary spiral sculpture present only as scalloped margins of axial; 3–4 scallops on spire whorls, 7–8 on final whorl, three pronounced scalloped cords in umbilicus. Secondary spiral sculpture of numerous, microscopic threads between axial cords, often worn away. Suture strongly indented. Aperture double, circular (2.8 mm in maximum width in neotype), barely solute. Inner lip smooth, erect. Outer lip expanded, narrower facing umbilicus, consisting of about five narrow, erect lamella, slightly auriculate. Shell dirty white with 6–7 spiral rows of widely separated, small, brown spots axially aligned; spots continue as bands over both sides of lip and form spots on inner lip. Operculum multispiral with a vertical, erect calcareous lamella.

Holotype: UF 451540.

Type locality: Near Morne Cavalier, Parc National Pic Macaya, 1 km W of Cay Michel, wet limestone outcrops, 1,191 m elevation, Department du Sud, Haiti, 18.3267° N, −74.0299° W.

Paratypes: UF 451537, Pic Formón, off path between Morne Cavalier and Cay Michel, Parc National Pic Macaya, wet limestone outcrops, 1,202 m elevation, Department du Sud, Haiti, 18.3254° N, −74.0262° W (1 specimen); OSUM 37269, Citadelle de Platons, cleared area around fortress, 727 m elevation, Department du Sud, Haiti, 18.2702° N, −73.9709° W (1 specimen); BMSM 17936, near Morne Cavalier, 1 km W of Cay Michel, wet limestone outcrops, 1,191 m elevation, Department du Sud, Haiti, 18.3267° N, −74.0299° W (1 specimen); OSUM 37270, near Morn Cavalier, Parc National Pic Macaya, foot of Mt. Ouasac, wet limestone outcrops in cleared forest, Department du Sud, Haiti, 1,341 m elevation, 18.3391° N, −74.0304° W (1 specimen).

Other Material Examined: Grego coll., Pic Formón, off path between Morne Cavalier and Cay Michel, Parc National Pic Macaya, wet limestone outcrops, 1,202 m elevation, 18.3254° N, −74.0262° W (8 specimens); Grego coll., near Morne Cavalier, Parc National Pic Macaya, 1 km W of Cay Michel, wet limestone outcrops, 1,191 m elevation, Department du Sud, Haiti, 18.3267° N, −74.0299° W (4 specimens); Grego coll., near Morne Cavalier, sinkholes in wet limestone forest, 1,116 m elevation, 18.3227° N, −74.0204° W (10 specimens); Grego coll., GTW 15157a, near Morn Cavalier, foot of Mt. Ouasac, wet limestone outcrops in cleared forest, 1,341 m elevation, 18.3391° N, −74.0304° W (4 specimens).

Distribution: Known only from the vicinity of Citadelle de Platons and Morn Cavalier at 727–1,341 m elevation.

Variation in specimens: Thirty-one specimens seen. The examples we have seen are very uniform in their characteristics, differing only in the number of axial lamellae (70–90).

Comparison with Other Species: See under *W. smithianum*, above.

Etymology: L. *macayaense*, from the area of Parc National Pic Macaya.

DISCUSSION

We have only Pfeiffer's unfigured description of *Choanopoma? smithianum* on which to base this species. Only four species, which we will refer to here as Species A, B, C, and D, were found at the type locality and surrounding areas (27 sites) despite careful examination.

All are members of *Weinlandipoma*. Pfeiffer's description, taken as a whole, contains enough information to identify which of these species represents *C. smithianum* based on circumstantial evidence. We present all available evidence below.

(1) Pfeiffer's description mentions his specimen being 11.5 mm long by 6 mm wide giving a length/width ratio = 1.9. Species A has a ratio of 1.7–1.9. Species B is more turbinate with a ratio of 1.2. Species C has a ratio of 1.4–1.7. Species D is 1.6–1.9. The length/width ratio of Pfeiffer's specimen most closely matches Species A and D.

(2) Pfeiffer's description mentions his specimen being 11.5 mm long in decollate length. Our specimens of Species A vary from 9.0–11.0 mm in decollate length. Species B varies from 8.8–11.3 mm in decollate length. Species C is the smallest with specimens ranging from 6.2–7.2 mm in decollate length. Species D is 7.2–9.6 mm in decollate length. The decollate length of Pfeiffer's specimen most closely matches Species A and B.

(3) Pfeiffer (1866: 88) referred to "*sutura costis excurrentibus irregulariter crenata*" in his original description. Species B has a set of cusps lining the suture of a uniform height, but often alternating with a smaller thread. Species A, C, and D have an undulating row of cusps of various lengths. Unfortunately, all four species could fit Pfeiffer's description.

(4) Pfeiffer compared his species with *Cyclostoma serraticosta* Weinland, 1862 and *Choanopoma puertoplatense* Pfeiffer, 1858. The former species was regarded as *Orcuttipoma rollei serraticosta* by Bartsch (1946), and as *Parachondria rollei serraticostus* by Watters (2006). The latter species was overlooked by Bartsch (1946) and Watters (2006) suggested it might be a *Colonina* based on the apparent spiral cords in the original minute (10 mm) illustration. (However, in view of Pfeiffer's comparison it is more likely that the spiral lines are bands of color rather than sculpture; this would eliminate this species from *Colonina* but the generic placement remains unknown as the type has not been located.) Pfeiffer also included where he would have placed his species in the 1865 second supplement to his *Monographia pneumonopomorum viventium*; he placed it at "7 1/2," in between *Cistula tractum* "Gundlach" (species 7) and *Choanopoma puertoplatense* (species 8). Both of these species resemble Species A, C, and D more so than Species B in having a prominent color pattern; however the same color pattern does occur in Species B but it is not as well-defined. Again, Pfeiffer's description of "*seriebus punctorum ruforum ornata*" could apply to any of the four species.

(5) Pfeiffer makes no note of the strongly scalloped axial cords seen in Species C and D.

(6) The outer lip is narrowly adnate in Pfeiffer's description of *C. smithianum*. Only Species A and B have adnate outer lips.

(7) The peculiar folded lamella of the peristome found in Species B, particularly in the Citadelle de Platons specimens, not seen in any other species of the genus, would certainly have been noted by Pfeiffer.

(8) Species D has not been found at the type locality.

Based on sculptural aspects, size, and degree of elongation we believe only Species A could fit the description of *Choanopoma ? smithianum* Pfeiffer, 1866. Species B is *W. gonavense* (Weinland, 1880), species C is *W. auduboni* and D is *W. macayaense*.

Weinlandipoma is restricted to the lower and middle elevations of the Chaîne de la Selle mountain range, which forms the Tiburon Peninsula and continues into the Barahona Peninsula as the Sierra de Baoruco (Figure 19). It is also found on the neighboring islands of Île de la Gonâve, Petite Gonâve, and Île à Vache. Species occur from Polo in the eastern Barahona Peninsula and Port-au-Prince across the Tiburon Peninsula to its western end. This mountain range originated apart from the rest of Hispaniola and continues to collide with it (with recently disastrous results). The mountain range harbors many unique species and genera of Annulariidae that do not seem to have counterparts in the remainder of Hispaniola. Watters (2006) hypothesized that these taxa evolved on what is now the Tiburon Peninsula before it merged with Hispaniola and that its taxa are not related to those on the rest of the island.

The radula of *Weinlandipoma* is typical of most annulariids, having a digitate first marginal (Figure 18). It is this tooth that varies most in the family (previously unpublished). Genetic studies of the Annulariidae are now being completed.

Weinlandipoma smithianum, *W. macayaense*, and *W. auduboni* may co-occur with *W. gonavense*, although *W. gonavense* appears to be more widespread. *Weinlandipoma smithianum* has been found in the vicinity of Camp Perrin at 200–210 m elevation (UF 32269, 48134), Citadelle de Platons at 727 m elevation, and at Pic Formón at 1,202 m elevation; it appears to occur at lower elevations than *W. auduboni* and *W. macayaense*. *Weinlandipoma auduboni* and *W. macayaense* are found near Morn Cavalier and Citadelle de Platons between 727–1400 m elevation. These sites have wet limestone outcrops and sinkholes in pine forests on the south slope of the Pic Macaya range (although much of this area has been deforested). Most of the sites are located within the Parc National Pic Macaya, which includes the last virgin cloud forest in Haiti and has as an extremely high level of endemism of plants and animals (Thompson, 1986; Grego and Šteffek, 2007; Fernández, 2007). *Weinlandipoma macayaense* and *W. auduboni* are sometimes, but not always, found together. The condition of the specimens does not permit a morphological examination of the genitalia but it is unlikely that the two species represent sexually dimorphic forms of one species; sexual dimorphism in shells is unknown in Hispaniolan annulariids.

Weinlandipoma gonavense is characterized by a peculiar apertural feature that is lacking in all other members

of the genus (Figures 13–17). Several of the lamella composing the outer lip are erect and folded back over toward the aperture to various degrees, sometimes forming a shelf. These folded lamella are usually among the middle lamella (although in some populations the lamella are outermost) and usually arise from the inner (axial) portion of the lip. The degree of folding varies considerably between and among populations, rarely absent, but is prominent in the Citadelle de Platons specimens. Specimens also vary in size, height, and color. This variability caused Grego and Šteffek (2007) to suggest that additional species occurred at their study sites. Thompson (1986) referred these taxa to *Weinlandipoma* sp. Bartsch (1946) divided this taxon into four subspecies, including one he did not formally name. These subspecies ranged from Île de la Gonâve to the southwestern coast of the Tiburon Peninsula. There appear to be two distinct forms in our study areas, one tall and pale that conforms to Bartsch's subspecies *conceptum*, the other short and dark and unnamed; some sites have both forms, others only one. Both forms have folded aperture lamella. However, a few specimens appear to be intermediate between the two groups. At this time we are referring to these specimens as *W. gonavense s.l.* although clearly more work is needed. A living individual of *W. gonavense* was figured in Fernández (2007, p. 195).

We believe the designation of a neotype of *Choanopoma ? smithianum* Pfeiffer, 1866, for the purpose of clarifying its taxonomic status is warranted at this time. The species seems to have a much narrower range than *Weinlandipoma gonaveuse*, with which it is occasionally found and potentially confused. It may be a significantly rare taxon deserving conservation protection that has not been recognized because of the lack of illustration or type specimens. Portions of its range have already been deforested. A neotype is chosen from the type locality and deposited at the Natural History Museum, London, UK as NHMUK 20120258. The type locality of "*in monte Platon insulae Haiti*" is here amplified as Citadelle de Platons, cleared area around fortress, 727 m elevation, Department du Sud, Haiti, 18.2702° N, −73.9709° W.

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LITERATURE CITED

Bartsch, P. 1946. The operculate land mollusks of the family Annulariidae of the island of Hispaniola and the Bahama Archipelago. Bulletin of the U.S. National Museum 192: 264 pp., 38 pls.

Clench, W.J. 1935. Some new Urocoptidae from Hispaniola. Proceedings of the Boston Society of Natural History 41: 1–12; pls. 1, 2.

Crosse, H. 1891. Faune malacologique terrestre et fluviatile de l'île de Saint-Domingue. Journal de Conchyliologie 39: 73–210.

Fernández, E. 2007. Hispaniola, a photographic journey through island biodiversity. Belknap Press, Cambridge, 374 pp.

Grego, J. and J. Šteffek. 2007. Biodiversity of Macaya National Park and Biosphere Reserve in conditions of global change. Pp. 85–112, in Proceedings from the Conference Stara Lesna Tatry Biosphere Reserve, Slovakia, 2–6 June 2007.

Henderson, J.B. and P. Bartsch. 1920. A classification of the American operculate land mollusks of the family Annulariidae. Proceedings of the U.S. National Museum 58: 49–82.

Kobelt, W. 1880. Die geographische Verbreitung der Mollusken. Jahrbücher der Deutschen Malakozoologischen Gesellschaft nebst Nachrichtsblatt 7(3): 241–286.

Pfeiffer, L. 1865. Monographia pneumonopomorum viventium, Supplementum Secundum. Theodor Fischer, Cassellis, 284 pp.

Pfeiffer, L. 1866. Beschreibung neuer Landschnecken. Malakozoologische Blätter 13: 76–91.

Pfeiffer, L. 1876. Monographia pneumonopomorum viventium, accedente fossilium enumeratione. Supplementum tertium, monographiae auriculaceorum. Parte secunda auctum. T. Fischer, Cassel, x + 479 pp.

Thompson, F.G. 1986. Land mollusks of the proposed National Parks of Haiti. Prepared for SAID/Haiti, Contract Number 521-0169-C-00-3083-00, 19 pp.

Tryon, G.W. 1867. Notices and reviews of new works. American Journal of Conchology 3(1): 82–103.

Watters, G.T. 2006. The Caribbean land snail family Annulariidae. Backhuys Publishers, Leiden. 557 pp.

Marionia kinoi (Nudibranchia: Tritoniidae): A new species from the tropical eastern Pacific

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ABSTRACT

Marionia kinoi, a new shallow water subtidal species of tritoniid nudibranch, is described from the tropical eastern Pacific. Along with a suite of internal characteristics (the number of rodlet rows on the jaw and a distinctively shaped rachidian tooth), its brilliant orange mid-dorsal color pattern, with whitish margins, immediately distinguish this new species from its Indo- and eastern Pacific congeners.

Additional Keywords: Gulf of California, Dendronotacea, Eusebio Francisco Kino

INTRODUCTION

The most recent comprehensive review of Tritoniidae taxonomy was published nearly 50 years ago (Odhner, 1963). Since then, new species descriptions have called into question his system of classification (e.g., Willan, 1988, and Smith and Gosliner, 2003, 2005, and 2007). When Bertsch et al. (2009) described the first species of Tritoniidae known to feed on zoanthid (not alcyonarid) Anthozoa, they presented a preliminary morphological phylogenetic analysis of the family. Their strict consensus phylogeny resulted in an unresolved polytomy of nine species, distributed among four genera (*Marionia*, *Tritonia*, *Tritoniella*, and *Tochuina*), emphasizing the need for further research to understand the evolutionary relationships within this group.

The present paper contributes to our understanding of the biodiversity of the tritoniids, essential for future comparative studies of this clade. There are less than 30 currently accepted species of named *Marionia* worldwide, with most occurring in the Indo-Pacific (Smith and Gosliner, 2007; Gosliner, Behrens and Valdés, 2008; García and Bertsch, 2009). Adding to the many unresolved taxonomic problems in this group, there are at least another 15 unnamed Indo-Pacific species (illustrated in Gosliner, Behrens and Valdés, 2008) and 2 unnamed eastern Pacific species, *Marionia* sp. 1 and *M.* sp. 2 (illustrated in Behrens and Hermosillo, 2005). Herein we name this *Marionia* sp. 1 from tropical west America.

MATERIALS AND METHODS

The specimens were relaxed in iced water until no response to external stimuli, then fixed in 4% Formalin. Dissection was performed by a dorsal incision through the length of the notum, from the base of the rhinophores to the base of the foot, allowing the removal of the entire visceral mass in one piece. The jaws and the radula were freed from the buccal mass, and put into 10% KOH solution. They were the rinsed in deionized water, air dried and coated for electron microscopy. Scanning electron micrographs (SEMs) were produced on a Hitachi model S-300D. Drawings were produced with the aid of a drawing tube attached to a stereo microscope. All drawings were digitalized by scanning and then composed and edited for publication using Corel Photoshop ™. The holotype and paratype specimens are deposited in the collections of California Academy of Sciences (CASIZ), San Francisco.

SYSTEMATICS

Suborder Dendronotacea Odhner, 1934
Family Tritoniidae Lamarck, 1809

Genus *Marionia* Vayssiere, 1877

Marionia kinoi new species
(Figures 1–10)

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Marionia sp. 1. Behrens and Hermosillo, 2005*; Hermosillo and Behrens, 2005; Hermosillo, 2006; Hermosillo et al., 2006*; Bertsch, 2010a.
Marionia sp. Camacho-Garcia, et al., 2005*.
* Indicates color photographs of living organisms included

Description: External Anatomy (Figures 1–2): Lengths of the living specimens were approximately 80mm. The color of the animal is light orange to brownish red, with small light colored tubercles that resemble a reticule that covers the surface of the dorsum. The sheaths and shafts of the rhinophores are orange, with the apical portions a light brown color. The body is elongate, subquadrilateral, with the largest section 1/3 of the distance to the posterior end of the foot. The oral veil extends beyond the front of the body. There are eight velar papillae on each side on the veil. The velar papillae are arranged in multifid groups, with blunt rounded apices. The body is finely granulated, except for the smooth sole of the foot. The rhinophores overhang from the margin of the notum. The rhinophore shafts are typically tritoniid, with a central clavus surrounded by a series of pinnate projections. The branchial plumes are relatively short. There are 11 plumes per side, with the largest in the middle third of the body. The branchial plumes are divided into four or five branches. The gonopore is located on the right side, at the first third of the body, below and between the 2nd and 3rd branchial plume. The anus is situated below the 3rd branchial plume, at the same height as the gonopore (Figure 2).

Digestive System: The jaws are yellowish brown in color, with a darker, reddish brown masticatory margin. The masticatory margin appears smooth to the naked eye, but scanning electron microscopy reveals the presence of three to four rows of jaw rodlets. The jaw rodlets at the anterior portion present three rows, which continue halfway, were the fourth row begins to project (Figure 3), until the posterior portion where the four rows are separated. The jaw rodlets are slightly conical, resembling a shark jaw (Figure 4). The radula of the paratype is large, with a formula of 45 (35.1.1.1.35) at its broadest point (Figures 5–7). The rachidian tooth is tricuspid, with a base roughly rectangular, and resembles the shape of an "M" (Figures 6–7). The central cusp is thick, asymmetrical, incised in the shape of a "V," with a profound canal that begins at the base and fades to the right side of the cusp. The top of the wedge forms two rectangular projecting ridges that present scars along their interior margins. The rows of teeth are arranged very closely together. The first lateral teeth insert at the base of the outer cusp of the rachidian tooth, and are differentiated from the remaining lateral teeth, being more heavily constructed, broader and curved. The remaining lateral teeth are straight to slightly curved, and relatively broad and stout. (Figures 5–6). The esophagus is half the size of the digestive gland, forming a broad straight tube slightly distended at the insertion of the stomach on the ventral side (Figure 8). The stomach is small, less than 0.5 cm in diameter. There are approximately 30–38 subquadrate (slightly more rectangular than square) stomach plates. They are light cream colored, with rounded corners and a smooth surface. The intestine exits the stomach from the anterior left portion, curving up around the anterior portion of the digestive gland towards the right, becoming wider for a portion before abruptly narrowing again to terminate in the anus. The large digestive gland is shaped like a chili pepper. The posterior portion has an anterior hollow that fits around the posterior stomach. The smaller anterior lobe covers the anterior portion of the stomach, and is connected to the posterior digestive gland.

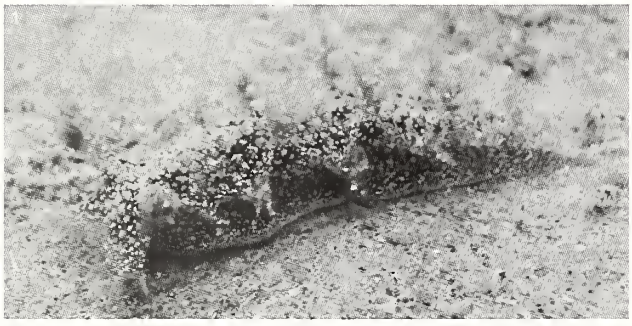


Figure 1. *Marionia kinoi* new species, photo of living specimen at type locality, 16 meters depth.

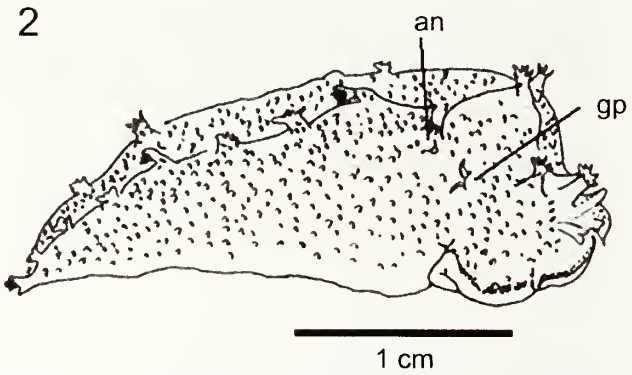
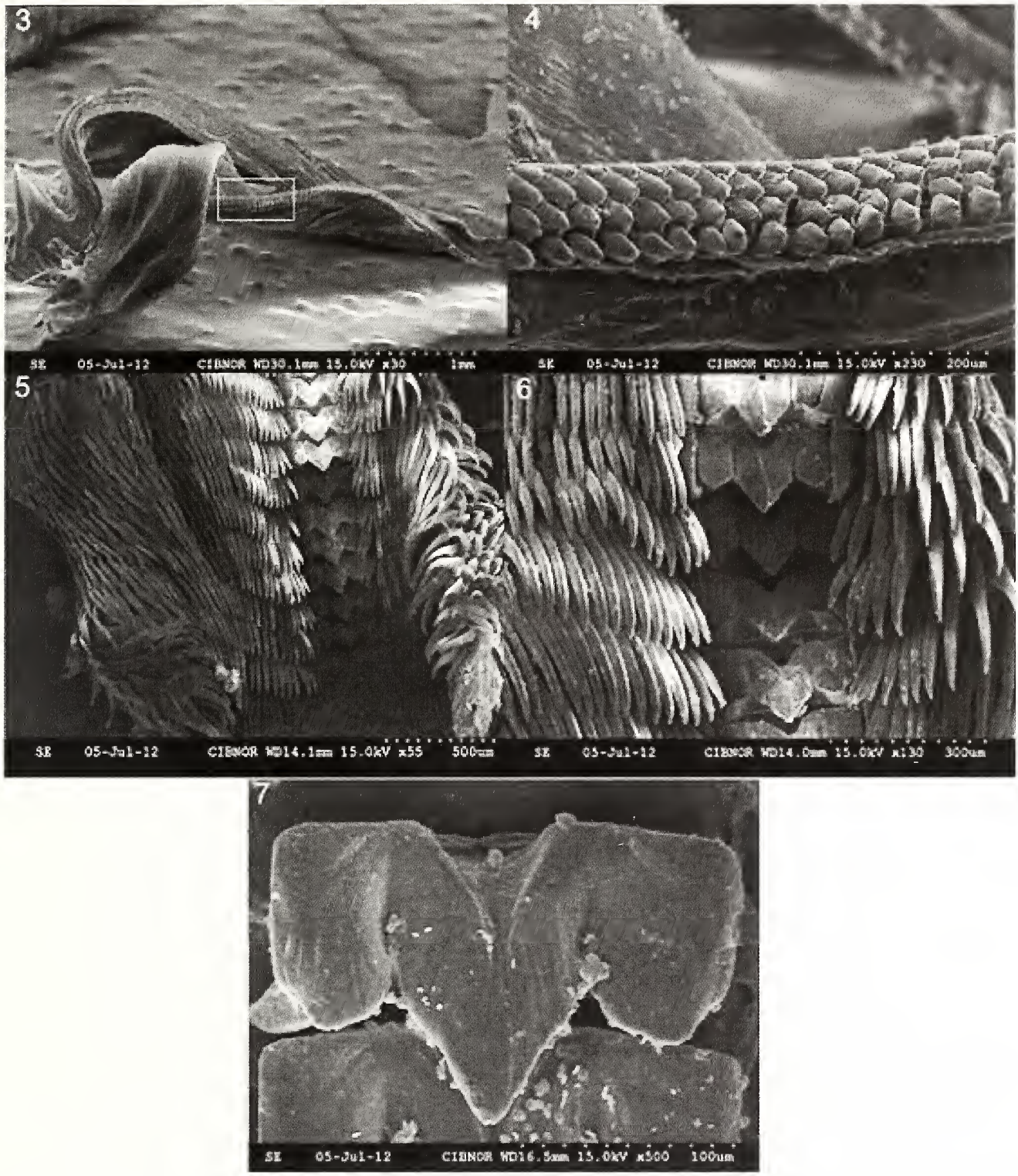


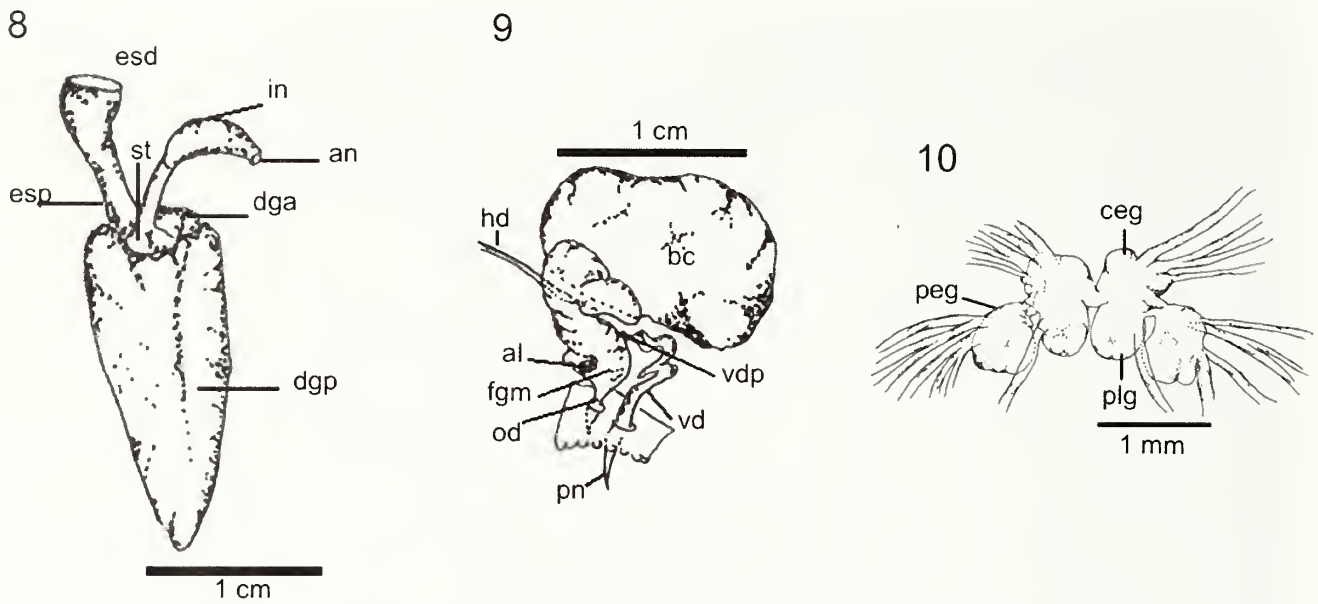
Figure 2. Lateral view of preserved specimen of *Marionia kinoi* new species. Abbreviations: **an,** anus; **gp,** gonopore.

Reproductive System: A narrow hermaphroditic duct connects to the narrow end of the ampulla (Figure 9). The ampulla is muscular and convoluted, wide and encased by the compact female gland mass. The smaller albumen gland is easily discernible from the membrane and mucus glands. The proximal vas deferens emerges from the female gland mass as a thin, curved tube. The distal portion slightly thickens before entering the base of the conical unarmed penis, lying near the gonopore. The muscular bursa copulatrix is an inflated oval 1.5 cm long. The vaginal duct is short, slightly widening at the vaginal atrium. The oviduct exits the female gland mass and opens to the vaginal atrium.

Nervous System: The ganglia of the central nervous system sits on the dorsal esophagus, just behind the buccal mass (Figure 10). The central nervous system is symetrical.



Figures 3–7. SEMs of jaw and radula of *Marionia kinoi* new species, paratype CASIZ 190511. **3.** Lateral view of the masticatory border, showing the arrangement of jaw rodlets. **4.** Detail of jaw rodlets. **5.** Eleven rows of the radula, entire half-rows. **6.** Closer view of rachidian and lateral teeth (five rows). **7.** Close-up of single rachidian tooth.



Figures 8–10. Drawings of internal anatomy of *Marionia kinoi* new species **8.** Visceral mass. **9.** Reproductive system. **10.** Central nervous system. Abbreviations: **al,** albumen gland; **am,** ampulla; **an,** anus; **bc,** bursa copulatrix; **dga,** anterior digestive gland; **dgp,** posterior digestive gland; **esd,** distal esophagus; **esp,** proximal esophagus; **fgm,** female gland mass; **gp,** gonopore; **hd,** hermaphroditic duct; **in,** intestine; **st,** stomach; **od,** oviduct; **pn,** penis; **va,** vaginal atrium; **vd,** distal portion of vas deferens; **vdp,** proximal portion of vas deferens.

The paired cerebral and pleural ganglia are distinct, joined by a short connective. The pedal ganglia are below and on either side of the cerebropleural ganglia, joined by short thick connectives.

Type Material: Holotype: 3.6 cm in length, CASIZ 190509; Paratypes: 3.8 cm length (dissected, CASIZ 190511) and 4 cm in length (CASIZ 190510), all from type locality, 9 March, 2011, Orso Angulo and Jorge Zarate coll.

Type Locality: Two miles south of Punta Arenas, on the Gulf of California coastline east of La Paz, near La Riviera, Baja California Sur, México (23°29′24″ N; 109°27′08″ W), 16 m depth.

Etymology: The specific name *kinoi* is given in honor of Padre Eusebio Francisco Kino, S.J. (1645–1711), the first Pacific conchologist (Baily, 1935), and intrepid explorer and cartographer of the Californias. His knowledge of the distribution of abalones was crucial for his determination that Lower California was a peninsula, not an island (Bertsch, 2010b). He founded the first Jesuit Catholic mission in the Baja California peninsula at La Paz, which however only functioned from 2 April to 14 July 1683 (Bertsch, 2011); no ruins are known to exist.

Distribution: *Marionia kinoi* new species is known from three eastern Pacific faunal provinces: the Sea of Cortez, Mexican and Panamic (*sensu* Briggs, 1974). It has been reported from the extreme southern portion of the Gulf of California (herein), from Bahía de Banderas, Jalisco/Nayarit (Hermosillo, 2006), Faro de Bucerías, Michoacán, and Ixtapa, Guerrero (Hermosillo and Behrens, 2005), Costa Rica (Behrens and Hermosillo, 2005), and the Islas Galápagos (Camacho-García et al., 2005).

DISCUSSION

Marionia kinoi new species has been included in the genus *Marionia* because of the number of rows in the jaw (3 to 4) and the presence of stomach plates, in accordance with the division proposed by Odhner (1963). Currently, the genus consists of 23 named Indo-Pacific species (compared and illustrated in Smith and Gosliner, 2007, and Gosliner, Behrens and Valdés, 2008), and five named species in the Atlantic (listed in García and Bertsch, 2009).

This new species can be distinguished readily from other species of *Marionia* based on coloration. For instance, *Marionia cyanobranchiata* (Rüppell and Leuckart, 1828), and *M. platyctenea* (Willan, 1988) have dark green brown or black gills. *Marionia distincta* Bergh, 1905, *M. levis* Eliot, 1904, *M. elongoreticulata* Smith and Gosliner, 2007, and *M. elongoviridis* Smith and Gosliner, 2007, have transverse light or dark lines on the dorsum. Among Atlantic species, the West African deeper-water species *M. vanira* Marcus and Marcus, 1966 has a green body, and the Caribbean *M. tedi* (Marcus, 1983) has a translucent white body and white processes.

Gills situated on a more prominently-thickened basal trunk separate *Marionia kinoi* new species from *M. rubra* (Rüppell and Leuckart, 1828), *M. dakini* (O'Donoghue, 1924), *M. arborescens* Bergh, 1890, and *M. pustulosa* Odhner, 1936.

The known feeding specificity of tritoniids on a single species or small group within a family of Octocorallia (Smith and Gosliner, 2003) reliably distinguishes *M. kinoi* new species from *M. hawaiiensis* (Pease, 1860), which preys on *Anthelia*, and *M. bathycarolinensis* Scott and Gosliner, 2005, a specific predator on *Paracis*. Neither of these prey genera of Octocorallia are known to occur in the Gulf of California (Hendrickx, Brusca, and Findley, 2005).

In addition to these features, there are two external characters that differentiate the plate-bearing tritoniids from our new species: the number of branchial plumes and the number of velar papillae. *Marionia kinoi* new species has 11 pairs of branchial plumes and eight pairs of compound velar papillae. None of the other 20 Pacific and two Atlantic species (contrasted in Table 1, Smith and Gosliner, 2007) has this suite of features. Moreover, the presence of 3 to 4 rows of jaw rodlets and 35 teeth rows distinguish *M. kinoi* new species from these congeners.

This new species differs from the only other known *Marionia* species occurring in the American Pacific; that still undescribed species is smaller in size, and the body, lateral processes, oral veil and rhinophores are white.

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LITERATURE CITED

Baily, Jr., J.L. 1935. The first Pacific conchologist. The Nautilus 48: 73–75.

Behrens, D.W. and A. Hermosillo. 2005. Eastern Pacific Nudibranchs. A Guide to the Opisthobranchs from Alaska to Central America. Sea Challengers, Monterey, 137 pp.

Bertsch, H. 2010a. Las conchas azules (the blue shells): Father Kino, abalones, and the island of California. The Nautilus 124: 188–191.

Bertsch, H. 2010b. Biogeography of northeast Pacific opisthobranchs: Comparative faunal province studies between Point Conception, California, USA, and Punta Aguja, Piura, Perú. In: Rangel Ruiz, L.J., J. Gamboa Aguilar, S.L. Arriaga Weiss, and W.M. Contreras Sánchez (compliadores). Perspectivas en Malacología Mexicana. Universidad Juárez Autónoma de Tabasco, Villahermosa: 219–259.

Bertsch, H. 2011. The missionary explorer-scientist, Father Eusebio Kino, S.J.: Faith, maps, sea shells and Mission San Xavier del Bac. Catholic Southwest, A Journal of History and Culture 22: 68–85.

Bertsch, H., Á. Valdés, and T.M. Gosliner. 2009. A new species of tritoniid nudibranch, the first found feeding on a zoanthid anthozoan, with a preliminary phylogeny of the Tritoniidae. Proceedings of the California Academy of Sciences 60: 431–446.

Briggs, J.C. 1974. Marine Zoogeography. McGraw-Hill, New York, 475 pp.

Camacho-García, Y., T.M. Gosliner, and Á. Valdés. 2005. Guía de Campo de las Babosas Marinas del Pacífico Este Tropical. California Academy of Sciences, San Francisco, 129 pp.

García, F.G. and H. Bertsch. 2009. Diversity and distribution of the Gastropoda Opisthobranchia from the Atlantic Ocean: A global biogeographic approach. Scientia Marina 73: 153–160.

Gosliner, T.M., D.W. Behrens, and Á. Valdés. 2008. Indo-Pacific nudibranchs and sea slugs: A guide to the world's most diverse fauna. Sea Challengers Natural History Books, Etc., Gig Harbor, Washington, and California Academy of Sciences, San Francisco, California. 426 pp.

Hendrickx, M.E., R.C. Brusca, and L.T. Findley. 2005. Listado y distribución de la macrofauna del Golfo de California, México. Parte 1. Invertebrados. A distributional checklist of the macrofauna of the Gulf of California. Part 1. Invertebrates. [Bilingual] Arizona-Sonora Desert Museum, Tucson, Arizona. xi + 429 pp.

Hermosillo, A. 2006. Ecología de los opistobranquios (Mollusca) de Bahía de Banderas, Jalisco-Nayarit, México. Ph.D. Tesis, CUCBA, Universidad de Guadalajara, 151 pp.

Hermosillo, A. and D.W. Behrens. 2005. The opisthobranch fauna (Gastropoda, Opisthobranchia) of the Mexican states of Colima, Michoacán and Guerrero: Filling in the faunal gap. Vita Malacologica 3: 11–22.

Hermosillo, A., D.W. Behrens, and E. Rios-Jara. 2006. Opistobranquios de México. Guía de babosas marinas del Pacífico, Golfo de California y las islas oceánicas. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Mexico, 143 pp.

Odhner, N. 1963. On the taxonomy of the family Tritoniidae. The Veliger 6: 48–52.

Smith, V.G. and T.M. Gosliner. 2003. A new species of *Tritonia* from Okinawa (Mollusca: Nudibranchia), and its association with a gorgonian octocoral. Proceedings of the California Academy of Sciences 54: 255–278.

Smith, V.G. and T.M. Gosliner. 2005. A new species of *Marionia* (Gastropoda: Nudibranchia) from the Caroline Islands. Proceedings of the California Academy of Sciences 56: 66–75.

Smith, V.G. and T.M. Gosliner. 2007. Two new species of *Marionia* (Mollusca: Nudibranchia) from the Indo-Pacific Region. The Veliger 48: 260–275.

Willan, R.C. 1988. The taxonomy of two host-specific, cryptic dendronotoid nudibranch species (Mollusca: Gastropoda) from Australia, including a new species description. Zoological Journal of the Linnean Society 94: 39–63.

Research Note

Omphalotropis ilapiryensis, a replacement name for *O. costulata* Emberton and Pearce, 1999 (Gastropoda: Littorinimorpha: Assimineidae)

Omphalotropis costulata Emberton and Pearce, 1999, from Madagascar, is a caenogastropod (operculate) land snail of the family Assimineidae. The genus is known from the central Pacific westward through the Indian Ocean, with Madagascar located at the extreme western edge of its distribution. Sixteen species of *Omphalotropis* are known from Madagascar (Pearce, 2003; Emberton 2004, 2009). *Omphalotropis costulata* Emberton and Pearce, 1999 has been reported from only two localities in a narrow geographical range where it is endemic to a single mountain range in southeastern Madagascar. The true ranges and conservation statuses of Madagascar's small, operculate land snails are very poorly known (Emberton, 2009) but the ongoing rapid destruction of rainforests in Madagascar poses serious conservation concerns to this and other species in Madagascar (Pearce, 2003).

We learned recently that the species name is a junior homonym of *Omphalotropis costulata* (Mousson, 1870), which occurs in Fiji, on Vanua Mbalavu Island. As per Art. 52.2 of the ICZN (1999), the junior homonym *Omphalotropis costulata* Emberton and Pearce, 1999 is an invalid name. No other synonym exists for this Malagasy species, so a replacement name is required (ICZN Art. 60.3). The species is currently listed in the IUCN Red List (Seddon, 2012) as *Omphalotropis* sp. nov. 2, a reversion to its original unassigned description in the literature (Emberton et al., 1996; Emberton, 1997). Here we assign it a replacement name.

Omphalotropis ilapiryensis new name

Omphalotropis 02 (as OM02)—Emberton et al., 1996: 210; Emberton, 1997: 1147, Table 5.

Omphalotropis sp. 2—Emberton, 1997: 1143 (and as "OM02" on p. 1147); Seddon, 2012

Omphalotropis costulata Emberton and Pearce, 1999: Emberton and Pearce, 1999: 370-371, figs. 25, 48; Pearce, 2003: 541, Table 8.10; Emberton, 2004: 84, 88, figs. 36-37, Table 3; *not Omphalotropis costulata* (Mousson, 1870: 190-191, pl. vii, fig. 10) [orig. *Realia (Omphalotropis) costulata*].

Type Material: *Omphalotropis costulata:* Holotype USNM 860791 (Emberton, 2004: 88); paratypes UF (Florida Museum of Natural History) 316989, 316990, 318440, 318441, 318442; all type material is from Mount Ilapiry.

Additional Material: Additional specimen UF 282795, cataloged at UF as from Ramabeafo Mountain (Emberton, 2004: 88, figs. 36-37).

Etymology: For its type locality, Mount Ilapiry (Vohimena Chain, Tulear Province, southeastern Madagascar; Emberton and Pearce, 1999).

Remarks: Ramabeafo Mountain (24.742° S, 46.854° E) is located 20.5 km NW from Mount Ilapiry (24.859° S, 47.011° E). Later, Emberton (2009: 20-21, figs. 119-121) used "*Omphalotropis* sp. 2" for a species found south of Antsahanoro in northeastern Madagascar, but it is certainly not the same species as *O. ilapiryensis* (which was formerly referred to as "*Omphalotropis* sp. 2").

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We acknowledge Carl Christensen, Mary Seddon, and Craig Hilton-Taylor (IUCN) for bringing the homonymy of *Omphalotropis costulata* to our attention. We are grateful to John Slapcinsky for assistance, including obtaining museum specimen records. We thank Mary Seddon and John Slapcinsky for reviewing the manuscript.

LITERATURE CITED

Emberton, K.C. 1997. Diversities and distributions of 80 land-snail species in southeastern-most Madagascan rainforests, with a report that lowlands are richer than highlands in endemic and rare species. Biodiversity and Conservation 6(8): 1137–1154.

Emberton, K.C. 2004. Madagascan *Georissa*, *Cyclotus*, *Omphalotropis* and so-called *Chondrocyclus* (Gastropoda: Caenogastropoda: Hydrocenidae, Cyclophoridae, Assimineidae). Archiv für Molluskenkunde 133(1-2): 69–107.

Emberton, K.C. 2009. Operculate land snails from three rainforest transects in northeastern Madagascar, with descriptions of nine new species and one new subspecies (Gastropoda: Caenogastropoda). Archiv für Molluskenkunde 138(1): 1–41.

Emberton, K.C. and T.A. Pearce. 1999. Land caenogastropods of Mounts Mahermana, Ilapiry, and Vasiha, southeastern Madagascar, with conservation statuses of 17 species of *Boucardicus*. The Veliger 42(4): 338–372.

Emberton, K.C., T.A. Pearce, and R. Randalana. 1996. Quantitatively sampling land-snail species richness in Madagascan rainforests. Malacologia 38: 203–212.

ICZN [International Commission on Zoological Nomenclature]. 1999. International Code of Zoological Nomenclature.

Fourth Edition. The International Trust for Zoological Nomenclature, London, xxix+ 306 pp.

Mousson, A. 1870. Faune malacologique terrestre et fluviatile des iles Viti, d'après les envois de M. le Dr. Édouard Graeffe. Journal de Conchyliologie 18 (1870): 109–135, part 2: 179-236, pls. VII-VIII. [in French]

Pearce, T.A. 2003. Gastropoda, terrestrial snails. In: Goodman, S.M. and J.P. Benstead (eds.). Natural History of Madagascar. University of Chicago Press, Chicago: 529–574.

Seddon, M.B. 2012. *Omphalotropis* sp. nov. 2. IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. http://www.iucnredlist.org/details/40081/0. (Access 23 Oct. 2012).

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A new species of *Solemya* (Bivalvia: Protobranchia: Solemyidae) from a hydrothermal vent in the Iheya Ridge in the mid-Okinawa Trough, Japan

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ABSTRACT

A new species, *Solemya* (*Solemya*) *flava*, is described from a hydrothermal vent field located in the Iheya Ridge in the mid Okinawa Trough, Japan. The small-sized new species is characterized by (1) a branched internal ligament attached to the chondrophore, (2) a bright yellowish brown periostracum, and (3) relatively short shell length relative to height (length/height = ca. 2.2) for solemyid bivalves. This species is associated with a vesicomyid clam, *Calyptogena okutanii* Kojima and Ohta, 1997, which is dominant in chemosynthetic environments.

Additional Keywords: taxonomy, *Acharax*, *Calyptogena* site

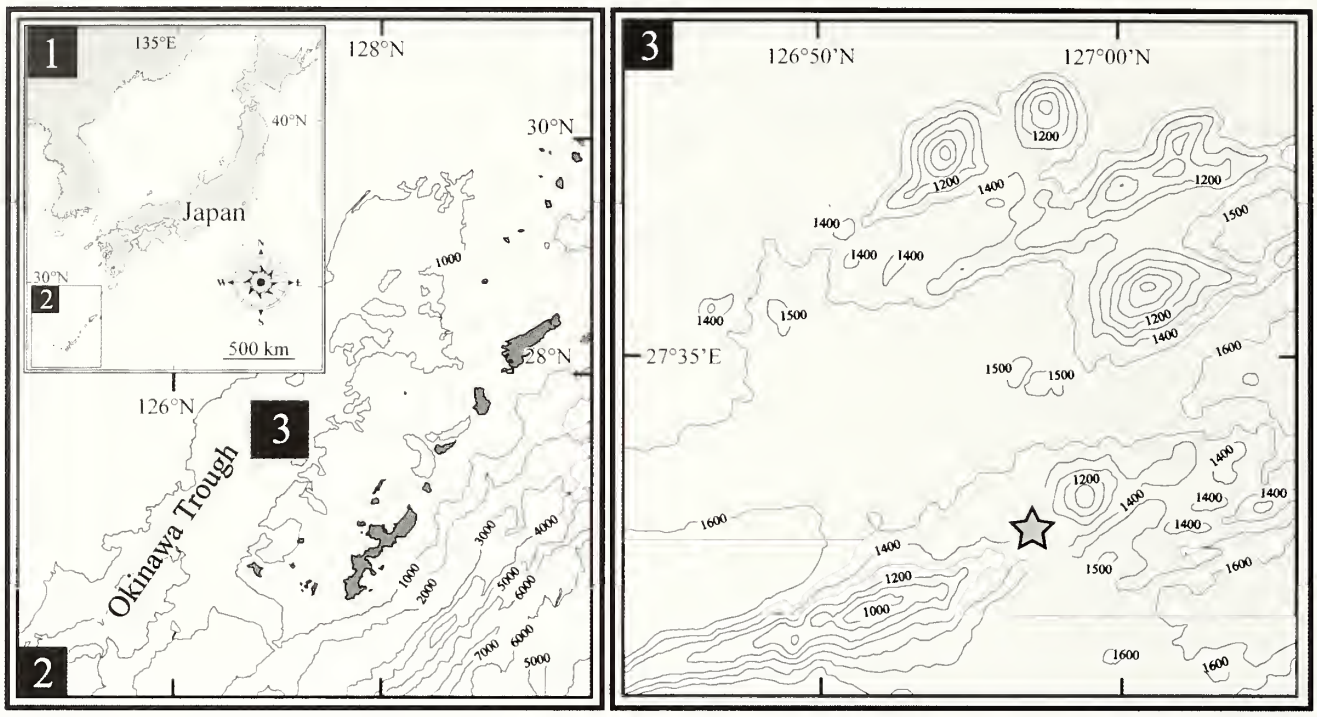
INTRODUCTION

Solemyids are an ancient group of bivalves whose fossil records date back to the Ordovician (Pojeta, 1988; Bailey, 2011). More than 30 Recent species are known (Huber, 2010), and there is also a rich fossil record for the group (e.g. Kiel, 2010; Amano and Ando, 2011; Taviani et al., 2011). They are morphologically characterized by an elongate shell with a thick periostracum, a posteriorly situated and toothless hinge, enlarged ctenidia, and reduced digestive system. The periostracum is much larger than the calcified part of the shell and folded inwards in living-animals. All known species are associated with reduced environments including vents and seeps, and they are one of several groups of chemosynthetic bivalves (Taylor and Glover, 2010), harboring sulfide-oxidizing chemoautotrophic bacteria in the ctenidia (Stewart and Cavanaugh, 2006).

Numerous chemosynthetic-based biological communities have been documented around Japan since 1980s (see review by Sasaki et al., 2005; Watanabe et al., 2010). Okinawa Trough is one of major localities with communities sustained by active hydrothermal vents. During a dive in the Iheya Ridge in mid-Okinawa Trough, an unknown species of the Solemyidae was collected. This was the first record of the family from the Okinawa Trough, and, as a result of morphological comparisons, the specimens were identified as a new species. In this paper we describe this new solemyid species colonizing the *Calyptogena* site.

MATERIALS AND METHODS

Three specimens of the new species were collected from 27°32.994′ N, 126°58.230′ E at a depth of 1402 m (Figures 1–3) with a scoop sampler from ROV Hyper-Dolphin operated by the Japan Agency for Marine-Earth Science and Technology (JAMSTEC). The specimens were collected together with sediments and *Calyptogena okutanii* during Dive #1246, February 10, 2011. The locality has been surveyed since the 1990s, and its fauna and bottom characters were documented by Ohta and Kim (2001). The specimens were preserved during the



Figures 1–3. The type locality of *Solemya (Solemya) flava* new species. **1.** Map of Japan showing location of Okinawa. **2.** Detailed map of Okinawa Trough; bottom contour intervals are 1000 m. **3.** Detailed bathymetrical map of the Iheya Ridge. Star indicates the type locality.

cruise at −30°C in light-shielded conditions, and fixed in 99% ethanol in the laboratory. All specimens used for description were dissected under a binocular microscope. The type specimens were registered in the Department of the Historical Geology and Paleontology, The University of Tokyo (UMUT).

SYSTEMATICS

Family Solemyidae Gray, 1840

Genus *Solemya* Lamarck, 1818

Solemya (Solemya) flava new species
(Figures 4–15)

Diagnosis: Branched internal ligament attached to the chondrophore, bright yellowish brown periostracum, and relatively short shell length relative to shell height for solemyid bivalves.

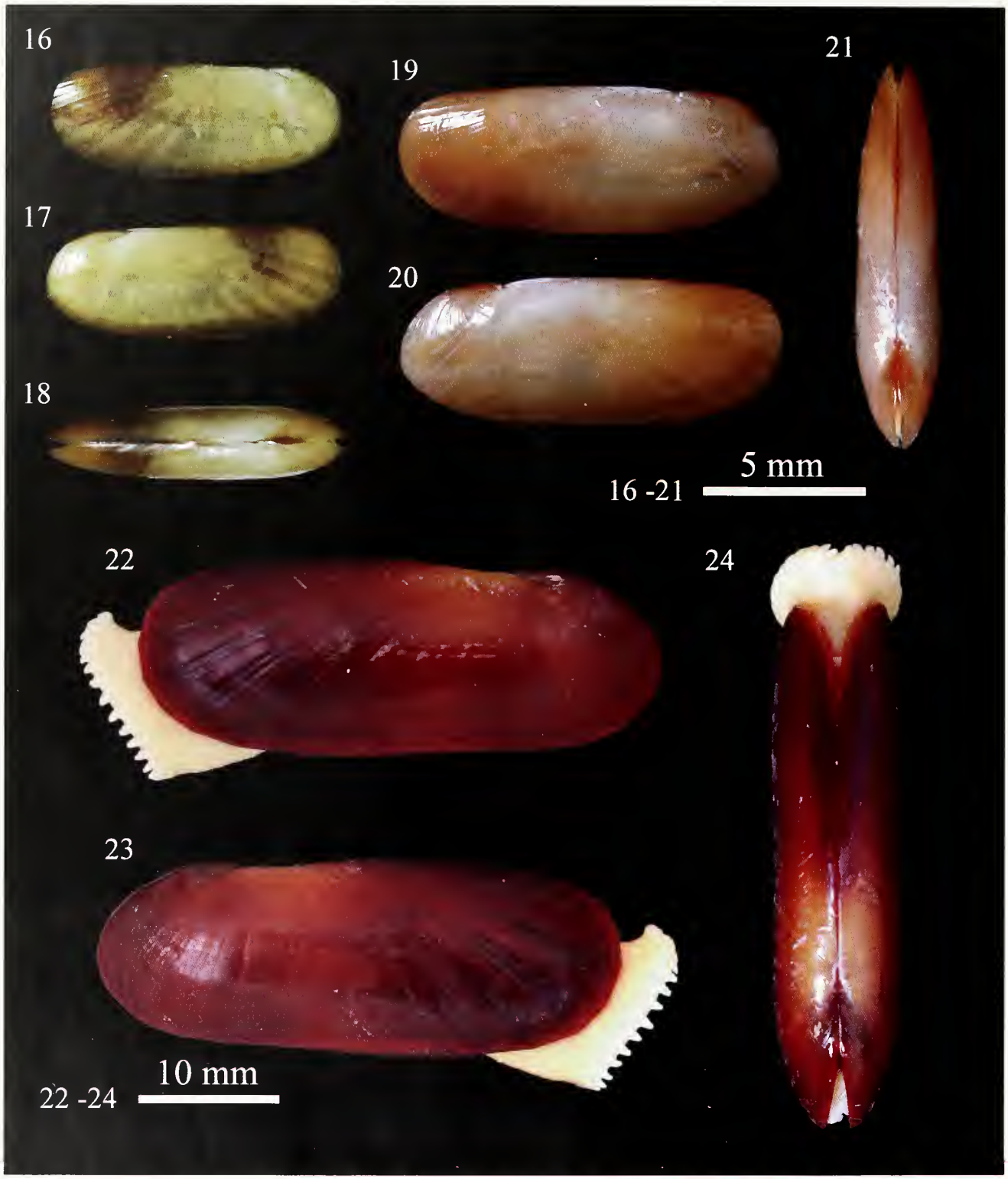
Description: Shell small, up to 14.2 mm in length, elongate oval, laterally compressed, equivalve, inequilateral, thin and flexible. Umbones not prominent, situated at posterior one-fourth of shell length. Lunule and escutcheon absent. Antero-dorsal margin straight, almost parallel to straight ventral margin. Both anterior and posterior margins gently rounded. Postero-dorsal margin slightly convex, positioned slightly below beak, with well-expressed radial, oblique flexure corresponding to attachment of chondrophore to inner shell surface. Shell length small relative to shell height (length/height = ca. 2.2) for solemyid bivalves. Periostracum thick, brownish yellow, extending beyond shell margins and forming frills. Surface with widely spaced weak radial ribs or furrows, especially on anterior and posterior regions. Internal surface dull white. Ligament internal, thin, subtriangular, moderately broad, attached to chondrophore, without expansion in front of chondrophore. Chondrophore weak, narrow, situated behind posterior adductor scar. Internal radial rib anterior to posterior adductor scar inconspicuous, narrow, extended from umbo and located anterior to posterior adductor scar. Anterior adductor scar large, angular-oval, feebly impressed. Posterior scar smaller, oval, not adjoining antero-ventral margin of chondrophore or extending behind chondropore. Pallial line obscure.

Type Material: Holotype, UMUT RM30147, 11.5 × 5.8 mm with periostracum, 10.7 × 4.6 mm excluding periostracum (Figures 4–7); paratype #1, UMUT RM30148, 15.4 × 9.3 mm with periostracum, 14.2 × 6.9 mm excluding periostracum, (Figures 8–11); paratype #2, UMUT RM30149, 13.1 × 6.9 mm with periostracum, 12.5 × 5.7 mm excluding periostracum (Figures 12–15).

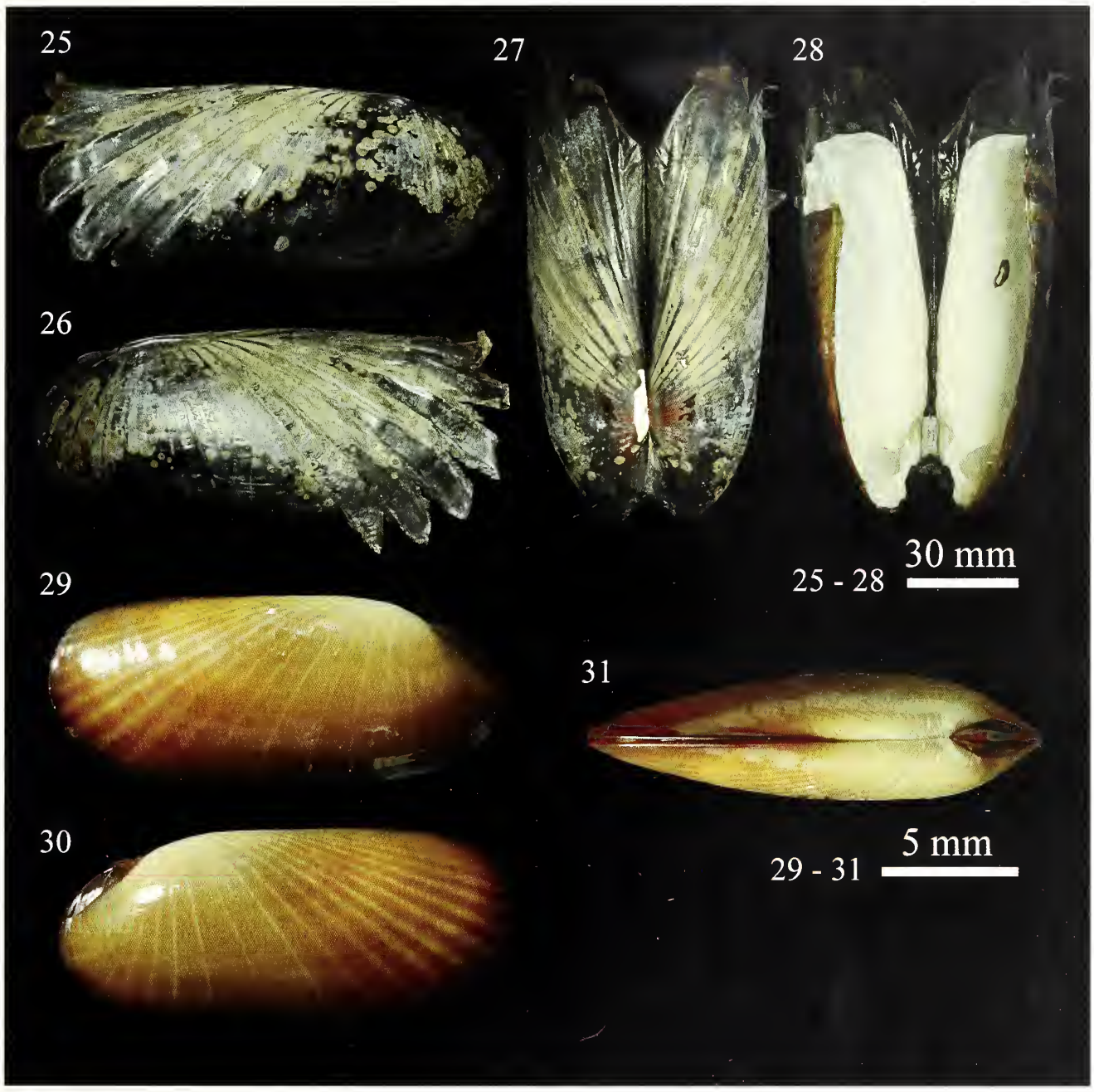
Type Locality: Iheya Ridge in the Okinawa Trough, 27°32.994′ N, 126°58.230′ E, 1402 m deep.

Distribution: Known only from the type locality.

Figures 4–15. *Solemya* (*Solemya*) *flava*. **4–7.** Holotype UMUT RM30147. **8–11.** Paratype #1 UMUT RM30148. **12–15.** Paratype #2 UMUT RM30149.



Figures 16–24. Solemyid bivalves for comparison (see also Sato et al., 2013). **16–18.** *Solemya* (*Solemya*) *pusilla* (Gould, 1861) UMUT RM 31050, Okinoshima-Island, Chiba Prefecture, Japan. **19–21.** *Solemya* (*Solemya*) *tagiri* Okutani, Hashimoto and Miura, 2004, one of paratypes JAMSTEC 031588-031594, Kagoshima Bay, Kagoshima Prefecture, Japan. **22–24.** *Solemya* (*Petrasma*) *pervernicosa* (Kuroda, 1948) JAMSTEC 053256, Joetsu Knoll, Niigata Prefecture, Japan.

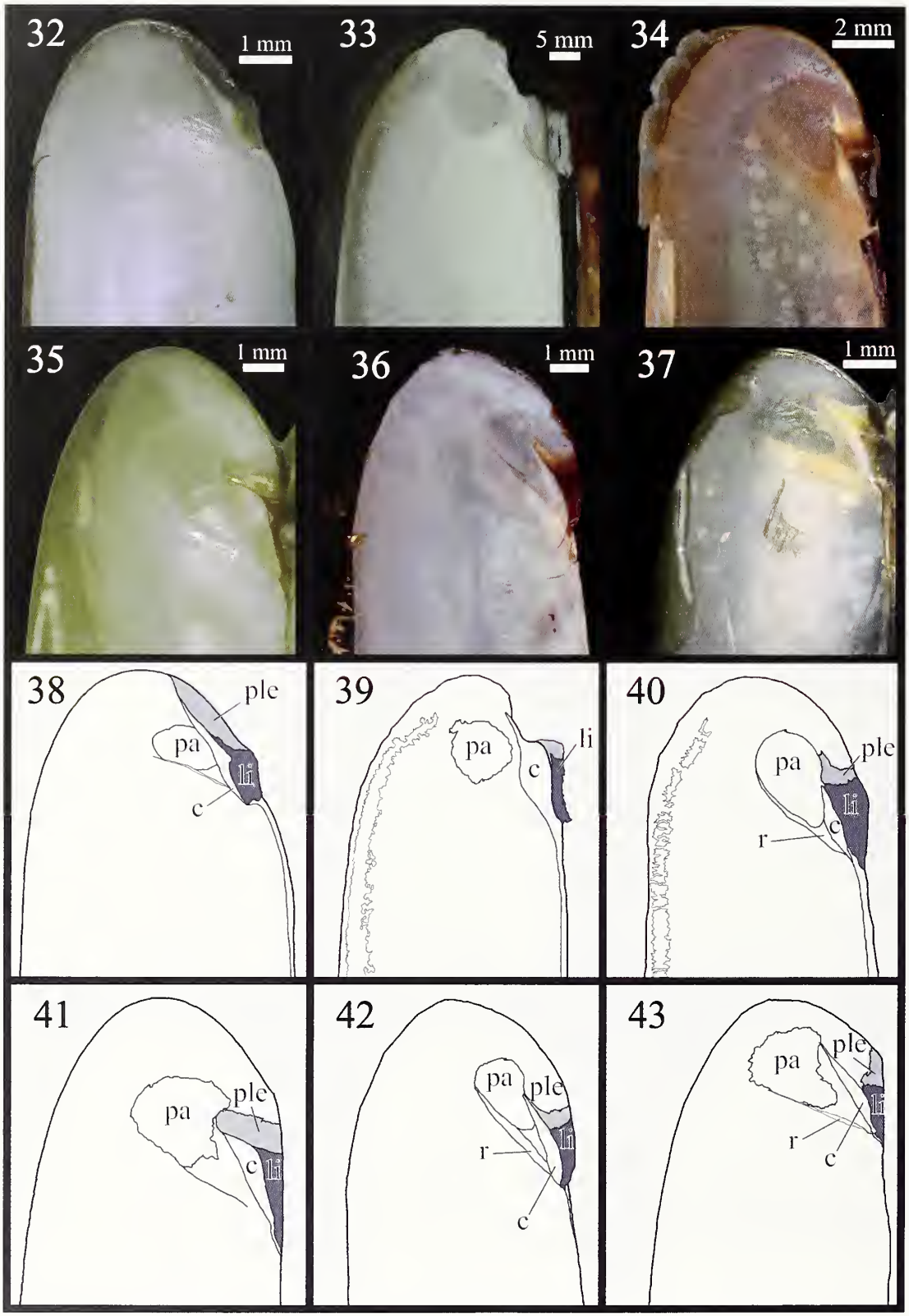


Figures 25–31. Solemyid bivalves for comparison (see also Sato et al., 2013). **25–28.** *Acharax johnsoni* (Dall, 1981) UMUT RM 28724. Off Otsuchi, Iwate Pref., Japan. **29–31.** *Acharax japonica* (Dunker, 1882) UMUT RM 30934. Shimoda Marine Research Center, Shizuoka Pref., Japan.

Etymology: The specific epithet is derived from the Latin word *flavus* meaning yellow.

DISCUSSION

The new species is assigned to *Solemya* (*Solemya*) on the basis of conchological characters. The genus *Solemya* is distinguished from another valid genus of the family, *Acharax* in having internal ligament and a slightly convex postero-dorsal margin (Dall, 1908). *Solemya* is divided into five subgenera: *Solemya*, *Solemyarina*, *Petrasma*, *Zesolemya*, and *Austrosolemya* (Dall, 1908; Cox, 1969; Taylor et al., 2008; Kamenev, 2009) which are diagnosed as follows by features near the umbo such as the posterior adductor muscle scar, internal ligament, chondrophore



Figures 32–43. Internal umbonal areas of six solemyid species around Japan. Images in Figures 32–37 are shown as diagrams in Figures 38–43. **32, 38.** *Acharax japonica*. **33, 39.** *Acharax johnsoni*. **34, 40.** *Solemya (Petrasma) pervernicosa*. **35, 41.** *Solemya (Solemya) pusilla*. **36, 42.** *Solemya (Solemya) tagiri*. **37, 43.** *Solemya (Solemya) flava* new species. Abbreviations: **c**, chondrophore; **li**, ligament; **pa**, posterior sdductor scar; **ple**, posterior outer-layer ligamental extension; **r**, internal radial rib.

Table 1. Comparisons among species of *Solemya* and *Acharax*.

Species	Maximum shell lenght (mm)	Lenght/ Height	Ligament situation	Posterior adductor muscle scar	Chondrophore	Internal radial rib	References
Solemya (Solemya) flava	14.2	2.18 (n=3)	internal	Deached from chondrophore and internal radial rib	Long, thin	Weak, branching from chondrophore at umbo	This study
Solemya (Solemya) pusilla	14.5	2.72 (n=2)	internal	Deached from chondrophore and internal radial rib	Long, thin	Very weak	Okutani (2000), Kamenev (2009)
Solemya (Solemya) tagiri	23.8	2.5 (n=11)	internal	Detached from chondrophore and internal radial rib but contacting with them	Long, thin	Weak, branching from chondrophore at umbo	Okutani et al. (2003)
Solemya (Solemya) valvulus	20.0	3.29 (n=1)	internal	Detached from chondrophore	Long, thin	Absent	Coan et al. (2000), Kamenev (2009)
Solemya (Petrasma) panamensis	47.0	2.88 (n=1)	internal	Attached to chondrophore and internal radial rib	Short, thin	Weak, narrow, supporting chondrophore	Kamenev (2009)
Solemya (Petrasma) pervernicosa	63.1	2.65 (n=4)	internal	Detached from chondrophore and internal radial rib	Short, thick	Strong, supporting chondrophore	Okutani (2000)
Acharax japonica	20.0	2.39 (n=43)	external	Poorly impressed	Absent	Very weak	Okutani (2000)
Acharax johnsoni	150.0	2.45 (n=2)	external	Well impressed	Absent	Absent	Coan et al. (2000)

and internal radial ribs: (1) *Solemya* s.s. has an opisthodetic internal ligament and a short and thin chondrophore; (2) *Solemyarina* has a heart-shaped internal ligament expansion in front of the week and narrow chondrophore. The posterior adductor scar is not impressed into the inner shell surface; (3) In *Petrasma*, the anterior end of the posterior adductor muscle scar is deeply impressed and attached to the anteroventral margin of the chondrophore; (4) *Zesolemya* is characterized by narrow posterior expansions of the ligament, a bifurcated chondrophore around the posterior adductor muscle scar, and prominent anterior linear extensions of the ligament; (5) *Austrosolemya* possesses an internal ligament with lobate anterior extensions, a broad triangular resilium, and strong chondrophoral ridges.

At the species level, the new species from off Okinawa should be compared with known solemyids from Japan and other adjacent regions of the Pacific geographically. Around Japan five species have been recorded (Kuroda et al., 1971; Habe, 1977; Okutani, 2000), namely *Solemya* (*Solemya*) *pusilla* (Gould, 1861) (Figures 16–18); *S.* (*S.*) *tagiri* Okutani, Hashimoto and Miura, 2004 (Figures 19–21); *S.* (*Petrasma*) *pervernicosa* (Kuroda, 1948) (Figures 22–24); *Acharax johnsoni* (Dall, 1981) (Figures 25–28), and *A. japonica* (Dunker, 1882) (Figures 29–31). *Solemya* (*S.*) *flava* is distinct from these species in five characters, viz. maximum shell length, ligament position, configuration of posterior adductor muscle scar, length and thickness of chondrophore, and internal radial ribs (Table 1). Species from other regions of the North Pacific (*Solemya* (*Solemya*) *valvulus*, *Solemya* (*Petrasma*) *panamensis*) are also distinguished by these characters (see also Table 1).

In *Solemya* (*Solemya*), two species, *S.* (*S.*) *pusilla* and *S.* (*S.*) *tagiri*, seem closely related to the new species in shell morphology. *Solemya* (*S.*) *pusilla* is most similar in maximum size to this species but differs in having a much more elongate outline (L/H = 2.72). *Solemya* (*Solemya*) *tagiri* is also similar in shell size and having a narrow and weak internal radial rib. However, the new species is distinguished from these species in having short shell length (L/H = 2.18) relative to shell height and umbo situation. The umbo of *S.* (*S.*) *tagiri* is situated in a more anterior position than that of this species. Internal umbonal areas of six solemyid species are illustrated in Figures 32–43 for comparison.

From an ecological standpoint, the new species might be related to *S.* (*S.*) *tagiri*, since both species are dependent on chemosynthesis-based, hydrothermal vent communities and their habitats are relatively geographically close in Japan. However, the habitat of *S.* (*S.*) *tagiri* is restricted to a narrow site at depth of 94–98 m in Kagoshima Bay which is nearly closed and isolated from the open ocean. In contrast, the locality of *S.* (*S.*) *flava* is isolated in the middle part of Okinawa Trough at a much greater depth (1402 m). Therefore, each species is possibly endemic to Kagoshima Bay and Okinawa Trough, respectively, and their habitats are sharply separated.

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LITERATURE CITED

Amano, K. and H. Ando. 2011. Giant fossil *Acharax* (Bivalvia: Solemyidae) from the Miocene of Japan. The Nautilus 125: 207–212.

Bailey, J. B. 2011. Paleobiology, paleoecology, and systematics of Solemyidae (Mollusca: Bivalvia: Protobranchia) from the Mazon Creek lagerstätte, Pennsylvanian of Illinois. Bulletins of American Paleontology 382: 1–72.

Coan, E.V., P.V. Scott, and F.R. Bernard. 2000. Bivalve Seashells of Western North America. Santa Barbara Museum of Natural History, Santa Barbara, 766 pp.

Cox, L.R. 1969. Superfamily Solemyacea. In: R.C. Moore (ed.), Treatise on Invertebrate Paleontology, Part N, Mollusca 6 (Bivalvia), Vol. 1. Geological Society of America and University of Kansas, Boulder, pp. 241–243.

Dall, W.H. 1908. A revision of the Solenomyacidae. The Nautilus 22: 1–2.

Habe, T. 1977. Systematics of Mollusca in Japan. Bivalvia and Scaphopoda. Hokuryukan, Tokyo, 372 pp. [in Japanese]

Huber, M. 2010. Compendium of Bivalves, Conchbooks, Hackenheim, 901 pp.

Kamenev, G.M. 2009. North Pacific species of the genus *Solemya* Lamarck, 1818 (Bivalvia: Solemyidae), with notes on *Acharax johnsoni* (Dall, 1981). Malacologia 51: 233–261.

Kiel, S. 2010. The fossil record of the vent and seep mollusks. In: Kiel, S. (ed.), The Vent and Seep Biota. Aspects from Microbes to Ecosystems. Springer, Dordrecht, pp. 255–277.

Kuroda, T., T. Habe, and K. Oyama. 1971 The Sea Shells of Sagami Bay. Maruzen, Tokyo, 489 pp. + 121 pls. + 489 pp. + 51 pp.

Ohta, S. and D. Kim. 2001. Submersible Observations of the Hydrothermal Vent Communities on the Iheya Ridge, Mid Okinawa Trough, Japan. Journal of Oceanography 57: 663–677.

Okutani, T. 2000. Family Solemyidae. In: Okutani, T. (ed.), Marine Molluscs in Japan. Tokai University Press, Tokyo, pp. 832–833.

Okutani, T., J. Hashimoto, and T. Miura. 2004. A new species of solemyid bivalves from near submarine fumaroles in Kagoshima Bay, Japan. Venus 62: 91–96.

Pojeta, J., Jr. 1988. The origin and Paleozoic diversification of solemyoid pelecypods. New Mexico Bureau of Mines & Mineral Resources Memoir 44: 201–222.

Sasaki, T., T. Okutani, and K. Fujikura. 2005. Molluscs from hydrothermal vents and cold seeps in Japan: A review of taxa recorded in twenty recent years (1984–2004). Venus 64: 87–133.

Sato, K., R. Nakashima, R. Majima, H. Watanabe, and T. Sasaki. 2013. Shell microstructures of five Recent solemyids from Japan (Mollusca: Bivalvia). Paleontological Research 17: 69–90.

Stewart, F.J. and C.M. Cavanaugh. 2006. Bacterial endosymbioses in *Solemya* (Mollusca: Bivalvia)—Model systems for studies of symbiont-host adaptation. Antonie van Leeuwenhoek 90: 342–360.

Taviani, M., L. Angeletti, and A. Ceregato. 2011. Chemosynthetic bivalves of the family Solemyidae (Bivalvia, Protobranchia) in the Neogene of the Mediterranean Basin. Journal of Paleontology 86: 1067–1076.

Taylor, J.D., E.A. Glover, and S.T. Williams. 2008. Ancient chemosynthetic bivalves: systematics of Solemyidae from eastern and southern Australia (Mollusca: Bivalvia). Memoirs of the Queensland Museum, Nature 54: 75–104.

Taylor, J.D. and E.A. Glover. 2010. Chemosymbiotic bivalves. In: Kiel, S. (ed.), The Vent and Seep Biota—Aspects from microbes to ecosystems. Springer, Dordrecht, pp. 107–135.

Watanabe, H., K. Fujikura, S. Kojima, J. Miyazaki, and Y. Fujiwara. 2010. Japan: Vents and seeps in close proximity. In: Kiel, S. (ed.), The Vent and Seep Biota. Aspects from microbes to ecosystems. Springer, Dordrecht, pp. 379–401.

A new shallow water species of *Nucinella* from the Philippines (Bivalvia: Protobranchia: Nucinellidae), member of a tropical seagrass chemosynthetic community

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ABSTRACT

A new species of the protobranch bivalve *Nucinella* is described from Panglao, central Philippines. It lives in very shallow seagrass habitats and co-occurs with other chemosymbiotic lucinid bivalves *Pillucina* and *Cardiolucina*. The species has been included in recent molecular phylogenies. For comparison details of hinge teeth are provided for the type species of *Nucinella*, *Pleurodon ovalis*, from the Pliocene of England.

Additional Keywords: protobranch, chemosymbiosis, new species

INTRODUCTION

Nucinellidae is a family of minute, mainly deep-water protobranch bivalves recently recognised as chemosymbiotic (Oliver and Taylor, 2012; Bieler et al., in press). Unusually, they are also all monomyarian, with only the anterior adductor muscle present. There are 21 known species in two genera comprising 15 *Nucinella* and 6 *Huxleyia* (La Perna, 2005; Oliver and Taylor, 2012). Identification of *Nucinella* is problematic on account of their small, smooth, external shells and species discrimination is largely based on hinge dentition and ligament form. Most are <5mm in height, with ovoid, smooth shells, often with a blue-green periostracum; the largest living species (25 mm) is *Nucinella boucheti* La Perna, 2005 described from 1600 m in the Philippines (La Perna, 2005). The ligament is external, either opisthodetic or amphidetic in *Nucinella* and internal opisthodetic in *Huxleyia*. The dentition is taxodont with up to 13 teeth located beneath the umbones and a larger and generally elongate, single anterior lateral tooth. There are persistent reports that *Huxleyia* species are dimyarian (e.g. Coan and Scott, 2012) but, after careful examination of several species, Oliver and Taylor (2012) were unable to confirm this and considered the genus monomyarian, as did Hayami and Kase (1993). Anatomically, nucinellids have large protobranch ctenidia, a large cleft foot that is deeply digitate at the margins and small, finger-like labial palps (Allen and Sanders, 1969; Kuznetsov and Schilyeko, 1984; Oliver and Taylor, 2012).

The depth distributions of living nucinellids are known to range from the interidal zone to 3580 m (Matsukuma et al., 1982; La Perna 2005; Oliver and Taylor, 2012) although the majority of records are from offshore to bathyal depths with *N. owenensis* Oliver and Taylor, 2012 found at 3400 m off Oman. Only a few species are known from very shallow water; *Huxleyia diabolica* (Jousseaume, 1897) is recorded from 6–40 m in seagrass and sand habitats of the northern Red Sea (Zuschin and Oliver, 2003) and *Huxleyia cavernicola* Hayami and Kase, 1993 is abundant in shallow sublittoral submarine caves of the Ryukyu Islands (Hayami and Kase, 1993). *Nucinella woodii* (Dall, 1898) lives in the Florida Keys at subtidal depths, 65 to 188 m (R. Bieler personal communication).

Reid (1990) speculated that nucinellids might be chemosymbiotic and the presence of bacterial symbionts in the ctenidial leaflets was later confirmed morphologically for two Indian Ocean species (Oliver and Taylor, 2012), by isotopic analysis of a New Zealand fjord species (McLeod et al., 2010) and the symbiotic Gammaproteobacteria identified molecularly (Bieler et al., in press) for *Nucinella giribeti* new species, described herein. Fossil monomyarian nucinellids, morphologically similar to living species, are recognized from the early Jurassic where they are often associated with dysaerobic environments (Harries and Little, 1999) and others reported from Mesozoic hydrocarbon seeps (Amano et al., 2007), with the likelihood that they were also chemosymbiotic.

The relationship of Nucinellidae to other protobranchs is still uncertain. Despite large morphological differences in the shells Allen and Sanders (1969) suggested a close

relationship with Solemyidae on the basis of anatomical similarity. Pojeta (1988) claimed a descent from Palaeozoic "solemyoideans" through the dimyarian *Manzanella* from the Permian. Since then nucinellids have been classified in the superfamily Manzanelloidea in the Solemyida, usually as the family Manzanellidae (Bieler et al., 2010). For reasons discussed in Oliver and Taylor (2012) we use the family name Nucinellidae for *Nucinella* and *Huxleyia* rather than Manzanellidae, which is based on the dimyarian Permian fossil *Manzanella* (Chronic, 1952). Recent molecular results provide little or no support for the monophyly of Solemyidae +Nucinellidae (Bieler et al., in press; Sharma et al., 2013).

We describe this new species from the Philippines, firstly, because it is one of the few *Nucinella* known from very shallow water and secondly, because it has been included in molecular and morphological analyses of bivalve phylogeny recorded only as *Nucinella* sp. (Bieler et al., in press, Sharma et al., 2013). The other nucinellid included in molecular analyses is *Huxleyia munita* (Dall, 1898) from the northeastern Pacific.

MATERIALS AND METHODS

Nucinella shells were collected in the Philippines during the Panglao 2004 Marine Biodiversity Project (see Bouchet et al., [2009] for details). They were found in a bulk sample collected by suction air-lift (station S11) and another single live-collected specimen from station S39 was used for molecular analyses by Bieler et al (in press).

Specimens were examined using Philips XL30 and FEI Quanta 650 scanning electron microscopes (SEM) following sputter coating in Au/Pd.

Institutional abbreviations used: MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMUK, Natural History Museum, London, U.K. Other abbreviations: H, height; L, length, PI, protoconch 1. All shell measurements in millimeters.

SYSTEMATICS

Subclass Protobranchia
Superfamily Manzanelloidea Chronic, 1952
Family Nucinellidae Vokes, 1956

Description: Shell obliquely oval, mostly higher than long. Hinge with sub-umbonal taxodont teeth and single, usually elongate lateral tooth on the anterior dorsal margin. Ligament mostly opisthodetic, wholly external or in a sunken resilifer. Shell sculpture of fine commarginal lirae; periostracum often glossy, persistent, rather thick. Monomyarian, only anterior adductor muscle present. Anatomy protobranch with large ctenidia (Allen and Sanders, 1969; Kuznetsov and Schileyko, 1984; Oliver and Taylor, 2012).

Remarks: The main difference between *Nucinella* and *Huxleyia* is the position of the ligament, external or slightly sunken in the former or wholly internal in the latter. For *Nucinella,* Oliver and Taylor (2012, fig. 7) showed that there is considerable variation between species in how deeply the ligament is sunken into the hinge plate.

Genus *Nucinella* Wood, 1851

Type Species: *Pleurodon ovalis* Wood, 1840, non *Pleurodon* Harlan, 1831. Syntype lots NHMUK Ramsholt L4465, Sutton L4464, L4618. Features of *N. ovalis*, probable syntypes, with details of the sub-umbonal teeth are illustrated in Figures 1–5.

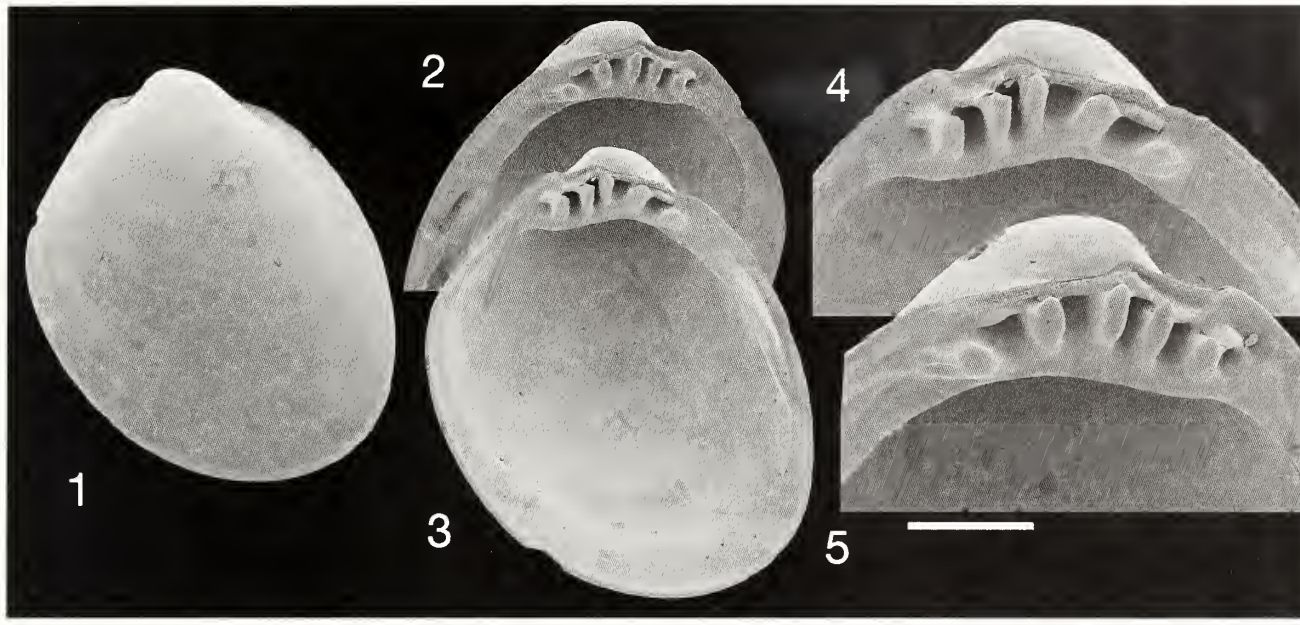
Diagnosis: As for the family, ligament external or in a shallow resilifer.

Remarks: See Vokes (1956) for details of type species designation. *Nucinella ovalis* is a Pliocene fossil first described from the Coralline Crag, Ramsholt and Sutton Members, Suffolk, England, (straddles Pliocene stage boundary of Zanclean and Piacenzian, 3.5–3.4 mya). Both localities have similar stratigraphy and the palaeoenvironment is thought to be offshore, shallow water to 50 m depth (Long and Zalasiewicz, 2011). Interestingly, *Nucinella* has been extinct since the Pleistocene in the northeastern Atlantic and Mediterranean (La Perna, 2004).

Nucinella giribeti new species
(Figures 6–17)

Description: Shell very small, largest valve L 2.8, H 3.9 (largest live shell L 2.3, H 3.0), equivalve, outline subovoid, external surface smooth with fine growth increments only, periostracum thick, *ca.* 5 µm, greenish, shell colour white. Protoconch, PI 148 µm long (holotype), sharp boundary to post-larval shell. Ligament opisthodetic short, set in shallow resilifer. Hinge, with 5–7 sub-umbonal teeth, slightly variable in size, younger individuals may have fewer teeth (Figures 15–16). Holotype (Figures 11–14) right valve with 7 sub-umbonal teeth, blade-like, slightly larger in posterior, anteriormost tooth very small; lateral tooth prominent, short, dorsal to adductor muscle scar; left valve with 6 sub-umbonal teeth, 2 posterior larger, anteriormost very small; lateral tooth as right valve. Anterior adductor muscle scar large, ovoid, posterior scar absent. Inner shell margin smooth. Image of live animal (Figure 6) shows extended, multidigitate foot.

Type Material: Holotype, whole shell, MNHN 26701, Figs 11–14, 17, L 2.0 H 2.7; Figured paratypes: Three whole shells: NHMUK 20130108, L 2.2, H 2.9 (Figure 7) and MNHN 26702, L 1.9, H 2.6; L 2.3, H 3.0 (Figures 8–9); MNHN 26703, 1 right valve, L 1.5 H 2.1 (Figure 10); 2 right valves (Figures 15,16). Other paratypes, 41 paired valves, 25 valves, MNHN 26704; 5 paired valves, 10 valves, NHMUK 20130108.



Figures 1–5. *Nucinella ovalis* (Wood, 1840), type species of *Nucinella* from Phocene, Coralline Crag, Ramsholt, Suffolk, England. Probable syntypes NHMUK L4465. **1.** Exterior or right valve, L = 1.5 mm. **2–3.** Interiors of right and left valves, L = 1.9 mm. **4–5.** Details of hinges of left and right valves. Scale bar = 300 μm.

Type Locality: Philippines, Panglao Island, lagoon off Poblacion 9°33.6′ N, 123°43.6′ E, 2 m, fine sand and seagrass, PANGLAO 2004, station S11.

Other Material Examined: Sequenced specimen from Philippines, Panglao Island, Tagbilaran-Panglao channel, 9°38.1′ N, 123°51.4′ E, 3–4 m, muddy sand beds of *Modiolus* sp., PANGLAO 2004, station S39. **GenBank numbers:** 18S rRNA: KC429324; 28S rRNA: KC429414; COI: KC429089.

Habitat and Distribution: Known only from or near the type locality in shallow water sand with seagrass.

Etymology: Named for Gonzalo Giribet, evolutionary biologist responsible for the first sequencing of Nucinellidae.

Remarks: The only other known species of *Nucinella* from the Philippines is *N. boucheti*, which occurs at depths of 1610–1580 m; this species, however, is much larger and has 13 sub-umbonal teeth (La Perna, 2005). In the tropical Indo-West Pacific three species of *Nucinella* are recorded from Japan (Matsukuma et al., 1982), a single species from off eastern Australia (Vokes, 1956), a larger species off Zanzibar (Thiele and Jaeckel, 1931), as well as the recently described *N. owenensis* from off Oman; all are from deeper water and differ in dentition from *N. giribeti*.

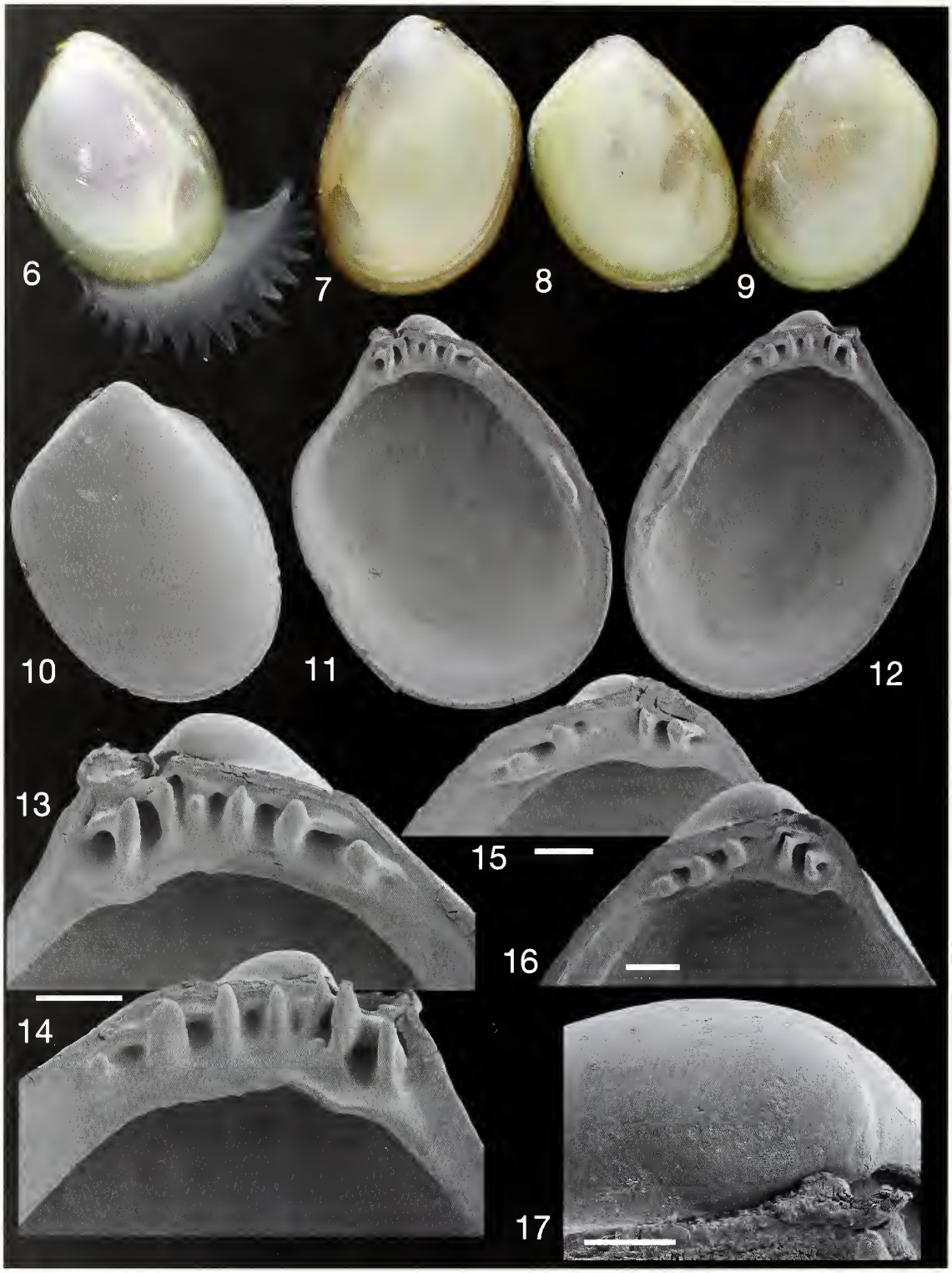
The type species of *Nucinella*, *Pleurodon ovalis* is a Pliocene fossil from the Coralline Crag of England that is similar in size and sub-umbonal dentition to *N. giribeti* but has a much longer anterior lateral tooth. (Figures 1–5).

DISCUSSION

Nucinella giribeti is the only species of the genus recorded from intertidal depths and it is very surprising that there are no other records from similar habitats in Southeast Asia. In all probability they have been overlooked because of their very small size, but the discovery in Panglao indicates that they can be quite abundant. The *N. giribeti* from the type locality were associated with chemosymbiotic lucinids *Pillucina* new species and *Cardiolucina siquijorensis*, both of which occurred in abundance in the seagrass sediments (Taylor and Glover, 1997; Glover and Taylor, in press). Both stations also contained several species of cardiids including *Fragum* spp., *Microfragum* spp., and *Fulvia* sp. (ter Poorten, 2009); other bivalves have yet to be studied.

Most nucinellids, along with many other protobranch mollusks, are found in deeper water from shelf to bathyal depths, with one of the deepest so far recorded being *Nucinella owenensis* recently described from 3400 m in an O_2 minimum zone, associated with deposit feeding and other chemosymbiotic bivalves (Oliver and Taylor, 2012). The Japanese species *Nucinella viridis* Matsukuma et al., 1983 was found at 3581 m at a likely hydrocarbon seep (Okutani and Iwasaki, 2003; Sasaki et al., 2005).

Life histories of Nucinellidae are poorly understood, but in common with other protobranchs, they are



Figures 6–17. *Nucinella giribeti* new species. **6.** Live specimen, 0–3 m Panglao Island, Philippines. Image by Pierre Lozouet MNHN. **7–9.** Paratypes. **7.** Left side (NHMUK 20130108), H = 2.9 mm. **8.** Right side, (MNHN 26702), H = 2.6 mm. **9.** Left side (MNHN 26702), H = 3.0 mm. **10.** Paratype, exterior of right valve (MNHN 26703), L = 1.5 mm, H = 2.1 mm. **11–12.** Holotype (MNHN 26701), interior of left and right valves, L = 2.0 mm, H = 2.7 mm. **13–14.** Holotype, detail of hinge teeth of left and right valves. Scale bar = 200 μm. **15.** Paratype, right valve, detail of hinge to show tooth variation (MNHN 26703). Scale bar = 200 μm. **16.** Paratype, right valve detail of hinge teeth (MNHN 26703). Scale bar = 200 μm. **17.** Protoconch of right valve of holotype. Scale bar = 50 μm.

presumed to have only lecithotrophic planktonic development. Protoconch sizes are variable: the type species *N. ovalis* is at least 210 µm, *N. giribeti* is 148 µm and *N. segnenzae* (Dall, 1898) (a Pleistocene fossil from Spain) is 260 m (La Perna, 2004).

Nucinella giribeti and *Huxleyia munita* (Eastern Pacific) are the first nucinellids to be included in molecular phylogenies of bivalves (Sharma et al., 2013; Bieler et al., in press), with results indicating a long independent history of these bivalves separate from the Solemyoidea. The pre-Mesozoic history of the Nucinellidae is uncertain but by early Jurassic times nucinellids, similar in morphology to living forms, were present in dysaerobic sediments (Harries and Little, 1999; Wignall et al., 2005) with later Cretaceous records from hydrocarbon seeps (Amano et al., 2007) indicating the high probability of early acquisition of chemosymbiosis in the family.

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LITERATURE CITED

Allen, J.A. and H.L. Sanders. 1969. *Nucinella serrei* Lamy (Bivalvia: Protobranchia), a monomyarian solemyid and possible living actinodont. Malacologia 7: 381–396.

Amano, K., R.G. Jenkins, and Y. Hikida. 2007. A new gigantic *Nucinella* (Bivalvia: Solemyoida) from the Cretaceous cold-seep deposit in Hokkaido, northern Japan. The Veliger 49: 84–90.

Bieler, R., J.G. Carter, and E.V. Coan. 2010. Classification of Bivalve Families. Pp. 113–133, in: Bouchet, P. and J.-P. Rocroi (2010) Nomenclator of Bivalve Families. Malacologia 52: 1–184.

Bieler, R., P.M. Mikkelsen, T.M. Collins, E.A. Glover, V.L. González, D.L. Graf, E.M. Harper, J. Healy, G.Y. Kawauchi, P.P. Sharma, S. Staubach, E.E. Strong, J.D. Taylor, I. Tëmkin, J.D. Zardus, S. Clark, A. Guzmán, E. McIntyre, P. Sharp, and G. Giribet. (In press). Investigating the Bivalve Tree of Life—an exemplar-based approach combining molecular and novel morphological characters. Invertebrate Systematics.

Bouchet, P., P.K.L. Ng, D. Largo, and S.H. Tan. 2009. PANGLAO 2004 - Investigations of the marine species richness in the Philippines. The Raffles Museum of Zoology, supplement 20: 1–19.

Chronic, H. 1952. Molluscan fauna from the Permian Kaibab Formation, Walnut Canyon, Arizona. Geological Society of America Bulletin 63: 95–166.

Coan, E.V. and P. Valentich-Scott. 2012. Bivalve seashells of tropical west America. Santa Barbara Museum of Natural History Monographs 6, Part 1, 597 pp.

Glover E.A. and J.D. Taylor. (In press). Lucinidae of the Philippines: highest known diversity and ubiquity of chemosymbiotic bivalves from intertidal to bathyal depths (Mollusca: Bivalvia: Lucinidae). Mémoires Muséum National d'Histoire Naturelle.

Harries, P.J. and C.T.S. Little. 1999. The early Toarcian (Early Jurassic) and the Cenomanian–Turonian (Late Cretaceous) mass extinctions: similarities and contrasts. Palaeogeography, Palaeoclimatology, Palaeoecology 154: 39–66.

Hayami, I. and T. Kase. 1993. Submarine cave Bivalvia from the Ryukyu Islands; systematics and evolutionary significance. The University Museum, University of Tokyo, Bulletin 35: 1–133.

Kuznetsov, A.P. and A.A. Schileyko. 1984. On the gutless Protobranchia (Bivalvia). Biologicheskie Nauki 2: 39–49. [in Russian with English abstract].

La Perna, R. 2004. *Nucinella alibrandi* (Conti, 1864) and *N. segnenzae* (Dall, 1898), the last European nucinellids (Bivalvia, Protobranchia). Rivista Italiana di Paleontologia e Stratigrafia 110: 571–577.

La Perna, R. 2005. A gigantic deep-sea Nucinellidae from the tropical West Pacific (Bivalvia: Protobranchia). Zootaxa 881: 1–10.

Long, P.E. and J.A. Zalasiewicz. 2011. The molluscan fauna of the Coralline Crag (Pliocene, Zanclean) at Raydon Hall, Suffolk, UK: palaeoecological significance reassessed. Palaeogeography, Palaeoclimatology, Palaeoecology 309: 53–72.

McLeod, R.J., S.R. Wing, and J.E. Skilton. 2010. High incidence of invertebrate-chemautotroph symbioses in benthic communities of the New Zealand fjords. Limnology and Oceanography 55: 2097–2106.

Matsukuma, A., T. Okutani, and R. Tsuchi. 1982. Three new species of the Nucinellidae (Bivalvia: Protobranchia) from Pacific coast of Japan. Venus 40: 177–186.

Okutani, T. and N. Iwasaki. 2003. Noteworthy abyssal molluscs (excluding vesicomyid bivalves) collected from Nankai Trough off Shikoku by the ROV Kaiko of the Japan Marine Science and Technology Center. Venus 62: 91–96.

Oliver, P.G. and J.D. Taylor. 2012. Bacterial symbiosis in the Nucinellidae (Bivalvia: Solemyida) with descriptions of two new species. Journal of Molluscan Studies 78: 81–91.

Pojeta, J. 1988. The origin and Paleozoic diversification of solemyid pelecypods. New Mexico Bureau of Mines and Mineral Resources Memoir 44: 201–222.

Poorten, J.J. ter. 2009. The Cardiidae of the Panglao Marine Biodiversity Project 2004 and the Panglao 2005 Deep-Sea Cruise with descriptions of four new species (Bivalvia). Vita Malacologica 8: 9–96.

Reid, R.G.B. 1990. Evolutionary implications of sulphide oxidizing symbioses in bivalves. In: Morton, B. (Ed.). The Bivalvia. Hong Kong University Press, Hong Kong. pp. 127–140.

Sasaki, T., T. Okutani, and K. Fujikura. 2005. Molluscs from hydrothermal vents and cold seeps in Japan: a review of taxa recorded in twenty recent years (1984–2004). Venus 64: 87–133.

Sharma, P.P., J.D. Zardus, E.E. Boyle, V.L. González, R.M. Jennings, E. McIntyre, W.C. Wheeler, R.J. Etter, and G. Giribet 2013. Into the deep: a phylogenetic approach to the bivalve subclass Protobranchia. Molecular Phylogenetics and Evolution 69: 188–204.

Taylor, J.D. and E.A. Glover. 1997. The lucinid bivalve genus *Cardiolucina* (Mollusca, Bivalvia, Lucinidae): systematics, anatomy and relationships. Bulletin of the Natural History Museum, London (Zoology) 63: 93–122.

Thiele, J. and S. Jaeckel. 1931. Muscheln der deutschen Tiefsee-Expedition. Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899, 21: 159–268.

Vokes, H.E. 1956. Notes on the Nucinellidae (Pelecypoda) with description of a new species from the Eocene of Oregon. Journal of Paleontology 30: 652–671.

Wignall, P.B., R.J. Newton, and C.T.S. Little. 2005. The timing of paleoenvironmental change and cause-and-effect relationships during the early Jurassic mass extinction in Europe. American Journal of Science 305: 1014–1032.

Wood, S.V. 1840. A catalogue of shells from the Crag. Magazine of Natural History series 2, 4: 230–234.

Wood, S.V. 1851. Monograph of the Crag Mollusca with descriptions of shells from the Upper Tertiaries of the British Isles volume II Bivalves. Palaeontographical Society Monographs 1–150.

Zuschin, M. and Oliver, P.G. 2003. Bivalves and bivalve habitats in the northern Red Sea: The northern bay of Safaga (Red Sea, Egypt): An actuopalaeontological approach, VI, Bivalvia. Naturhistorisches Museum, Wien, 304 pp.

Vertigo marciae (Gastropoda: Vertiginidae), a new land snail from Jamaica

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ABSTRACT

Vertigo marciae, a new species of gastropod mollusk (Pupilloidea: Vertiginidae), is described from Jamaica. This species is known in the Recent fauna only from John Crow Peak in the Blue Mountains, but also occurs as a Pleistocene fossil at Red Hills Road Cave. *Vertigo marciae* has been confused with *Vertigo gouldii*, but differs by its smaller shell size, lack of distinct shell striation, lack of an angular lamella, and presence of a flared aperture base. DNA sequence analyses document that *V. marciae* possesses unique mtDNA and nDNA sequences and is most closely allied with *Vertigo alabamensis*, *Vertigo hebardi*, and *Vertigo oscariana*. This group of species comprises a highly supported clade whose members are limited either to the Caribbean or the southeastern USA.

Additional Keywords: Vertigo, biogeography, southeastern USA, Caribbean, DNA sequence analysis

INTRODUCTION

In their synopsis of the Jamaican land snail fauna, Rosenberg and Muratov (2006) reported three species from the genus *Vertigo*, all of which possess ranges extending into the eastern half of North America (Nekola and Coles, 2010): *V. gouldii*, *V. milium*, and *V. ovata*. However, images of putative Jamaican '*V. gouldii*' on the Discover Life website (http://pick4.pick.uga.edu/mp/20q?search=Vertigo+gouldii&guide=1) illustrate a shell quite unlike *V. gouldii* from eastern North America (Nekola and Coles, 2010) in its light-yellow shell color, lack of sharp shell striation, and absence of a basal lamella. Observation of the three known Jamaican lots for this entity in the Academy of Natural Sciences of Philadelphia (ANSP) collections confirmed these differences. Although they looked most like *V. hebardi* Vanatta, 1912 of the Florida Keys, these lots clearly differed from that species by their taller shell, reduced striation, and absence of an angular lamella. Thus, rather than representing a population of *V. gouldii* isolated by 2000 km from its nearest neighbors (Nekola and Coles, 2010), these specimens appear to represent an undescribed new species. Based on shell descriptions, reports of *Vertigo gouldii* from the Pleistocene Red Hills Road Cave deposits of Jamaica (Paul and Donovan, 2005) also appeared to represent this new species. This conclusion was subsequently confirmed via observation of digital images.

We therefore investigated this putative new species via analyses of both shell morphology and DNA sequence data, and are now in the unusual situation of describing and reporting a new species simultaneously from both living and fossil material, while also being able to report on its phylogenetic relationships.

MATERIALS AND METHODS

Field Collection: The three known Recent lots of the putative new Jamaican species (ANSP 402244, 403039, and 403040) were collected on John Crow Peak in the Blue Mountains of eastern Jamaica on May 22, 1999, during the Jamaican Biotic Survey. Collecting methods were detailed in Rosenberg and Muratov (2006), and included drying of soil litter samples over a Berlese Funnel. This encouraged snails to enter aestivation, allowing them to mummify upon death. For this reason, it was possible to successfully extract, amplify, and sequence selected amplicons from both their mitochondrial and nuclear genomes (Nekola et al., 2009).

Shell Measurements: Measurements were determined in 0.1 mm increments for adult shells with aperture facing up, using a dissecting microscope with a calibrated ocular micrometer. Height and width were measured as the dimensions of a bounding box with long axis parallel to the shell axis and sides tangent to the tip of the protoconch, the base of the lip, the right-most margin of the aperture and the left-most margin of the body whorl.

Imaging: Shells were imaged at 20× magnification using a digital camera attached to a stereomicroscope.

Approximately 14 separate 1388×1040 pixel images were made of each specimen with the image focal lengths positioned at 75 µm increments from the front to back of the shell. CombineZ5 freeware (http://www.hadleyweb.pwp.blueyonder.co.uk/CZ5/combinez5.htm) was used to assemble a final image from the focused parts of each separate image. Assembled images were imported into Adobe Photoshop, where brightness and contrast were optimized and the background made uniformly black. These images were then compiled into a single plate.

DNA Sequence Analysis: Mitochondrial cytochrome b (*CytB*), 16S ribosomal RNA (*16S*) and the internal transcribed spacers 1 (*ITS-1*) and 2 (*ITS-2*) of the nuclear ribosomal RNA gene were investigated to test the distinctiveness of the putative new Jamacian species and to resolve its nearest evolutionary neighbors. The mitochondrial cytochrome oxidase subunit 1 (*CO1*) was not analyzed as we were unable to amplify this gene in the Jamaican species.

Sixteen specimens were chosen for analysis (Table 1). This set includes not only two specimens of the Jamaican species but also *Vertigo alabamensis*, *V. gouldii*, *V. hebardi*, and *V. oscariana*. We attempted to maximally spread these individuals across the known geographic range of each species (see Nekola and Coles, 2010). Because *V. conecuhensis* is likely a simple shell form of *V. alabamensis* (Nekola and Coles, 2010), only a single individual of this taxon was included. Topotype or near-topotype material was selected for *V. conecuhensis* (Pond Creek, Covington Co., Alabama, about 50 km from the type locality in Evergreen, Alabama) and *V. hebardi* (Long Key, Florida which is the type locality). Previously analyzed *16S* sequence data from three *Vertigo gouldii* specimens analyzed by Nekola et al. (2009) were retrieved from GeneBank (Table 1). *Vertigo pusilla*, the type species of the genus, was also included, as were *Gastrocopta cristata* and *Pupilla muscorum* for outgroup comparisons.

Genomic DNA was extracted from live, ethanol-preserved, or mummified material using the OmegaBioTek Mollusk DNA Extraction Kit. Because shell destruction was required, all shells were imaged prior to extraction using the methods detailed above. PCR amplification and sequencing of *CytB*, *16S*, *ITS-1*, and *ITS-2* were accomplished using standard methods (Nekola et al., 2009). Resultant traces were examined, primer ends removed, and aligned by eye. Because of their lower evolutionary rates, the nDNA *ITS-1* and *ITS-2* regions were concatenated to provide a roughly similar number of nucleotide differences to either of the mtDNA amplicons. Mega 5.0 (Tamura et al., 2011) was used to calculate the average number of nucleotide differences in the *CytB*, *16S*, and concatenated *ITS-1* + *ITS-2* regions between all putative species-level taxa. Substitutions included both transitions and transversions with pairwise gap deletion.

Table 1. Specimen information for material used in DNA sequence analysis.

Taxon					
		GENBANK Accession number			
Location	Latitude/Longitude	*CytB*	*16S*	*ITS-1*	*ITS-2*
Vertigo marciae new species					
John Crow Peak, St. Andrew Parish, Jamaica	18.1132 N., 76.6685 W.	KF214513	KF214503		
John Crow Peak, St. Andrew Parish, Jamaica	18.1132 N., 76.6685 W.	KF214514	KF214502	KF214489	KF214477
Vertigo alabamensis Clapp, 1915					
Johnson Mill Bay, Bladen Co., North Carolina, USA	34.7125 N., 78.5261 W.	KF214515	KF214501	KF214490	KF214478
Wolf Trap Bay, Leon Co., Florida, USA	30.3680 N., 84.5700 W.	KF214516	KF214500	KF214491	KF214479
Vertigo conecuhensis Clapp, 1915					
Pond Creek, Covington Co., Alabama	31.1036 N., 86.5343 W.	KF214517	KF214499	KF214492	KF214480
Vertigo gouldii (A. Binney, 1843)					
Brush Creek Canyon, Fayette Co., Iowa, USA	42.7796 N., 91.6890 W.	KF214508	GQ921506	KF214484	KF214472
Panther Creek, Searcy Co., Arkansas, USA	36.0858 N., 92.5649 W.	KF214509	GQ921507	KF214485	KF214473
11-Point River, Oregon Co., Missouri, USA	36.7931 N., 91.3334 W.	KF214510	KF214506	KF214486	KF214474
Vertigo hebardi Vanatta, 1912					
Long Key, Monroe County, Florida, USA	24.8146 N., 80.8211 W.	KF214511	KF214505	KF214487	KF214475
Elliott Key, Miami-Dade County, Florida, USA	25.4553 N., 80.1925 W.	KF214512	KF214504	KF214488	KF214476
Vertigo oscariana (Sterki, 1890)					
Blanchard Springs, Stone Co., Arkansas, USA	35.9582 N., 92.1778 W.	KF214518	KF214498	KF214493	KF214481
Wadboo Creek, Berkeley Co., South Carolina, USA	33.1971 N., 79.9461 W.	KF214519	KF214497	KF214494	KF214482
Vertigo pusilla Müller, 1774					
Podyji National Park, Moravia, Czech Republic	48.8586 N., 15.8960 E.	KF214520	KF214496	KF214495	KF214483
Gastrocopta cristata (Pilsbry and Vanatta, 1900)					
Albuquerque, Bernalillo Co., New Mexico, USA	35.0727 N., 106.6160 W.	KF214522	JN941032		
Pupilla muscorum (Linnaeus, 1758)					
Masaryk University, Brno, Moravia, Czech Republic	49.2509 N., 16.5738 E.	KF214521	KF214507		

Mega 5.0 was used to conduct nearest–neighbor joining (NNJ), maximum parsimony (MP), and maximum likelihood (ML) trees for the three focal regions. NNJ was based on Maximum Composite Distance including transitions and transversions with pairwise gap deletion. MP used the close neighbor interchange search option with the random addition of 10 replicate trees. ML used all sites and was based on the Tamura–Nei substitution model, a five–category Gamma Distribution for substitution rates, and the Nearest Neighbor Interchange ML heuristic method. In all cases support values were estimated from 1000 bootstrap replicates. Additionally, Bayesian trees were generated using MrBayes 3.1 (Huelsenbeck and Ronquist, 2001) using a GTR substitution model assuming gamma-shaped rate variation over 1,000,000 generations with a sampling frequency of once each 1000 generations.

Nomenclature: Taxonomic names and concepts follow Nekola and Coles (2010). Apertural lamellae and fold nomenclature follows that of Pilsbry (1948: 869, fig. 469), i.e., parietal "teeth" are referred to as "folds" and all other "teeth" are termed "lamellae", whatever their form. Also, we follow Pilsbry (1948) by referring to the raised riblets on the surface of *Vertigo* shells as "striae."

SYSTEMATICS

Class Gastropoda
Subclass Pulmonata
Order Stylommatophora
Family Vertiginidae

Genus *Vertigo* Müller, 1773

Vertigo marciae new species
(Figures 1–6; Tables 1, 2)

GenBank Accessions KF214477, KF214489, KF214502, KF214503, KF214513, KF214514

Diagnosis: Minute shell reminiscent of *Vertigo hebardi* but taller, less striate, and lacking angular lamella; shell surface smooth and glossy with indistinct wrinkles; aperture flared toward bottom; four lamellae/folds present, including parietal, columellar, and two palatals.

Description: Shell 1.4–1.6 mm tall × 0.8–1.0 mm wide (holotype 1.5 × 0.8 mm), columnar-ovoid to ovoid, approximately 4–4.5 whorls, with moderately shallow suture and domed apex. Translucent, pale yellow-brown color. Body whorl approximately 60% of total height (Figures 1–3, 5, 6). Protoconch and neanic whorls smooth (Figure 4), with subsequent whorls having irregular, infrequent, and weak wrinkles. Immediately behind aperture sculpture takes the form of irregular low striae (Figure 2). Aperture flared on bottom, making it taller than wide and approximately 1/3 of shell height. Lip unthickened and slightly reflexed, sinulus moderate-weak, sometimes expressed as simple flattening of palatal wall. Basally aperture abruptly inflates to form rounded swelling but not crest (Figure 4). Umbilicus closed (Figure 3). Aperture with four lamellae/folds: parietal lamella strong, slightly sinuous (Figures 1, 2, 5, 6); columellar lamella downward-sloping, peg-shaped; two palatal folds with lower being approximately twice as long as upper and extending approximately 0.2 whorls into body whorl, lower slightly more immersed than upper, both highest at mid length (Figures 1, 2, 5, 6). Apertural end of lower palatal fold coincides with abrupt inflation of basal aperture. Externally shell only slightly impressed over palatal folds (Figure 4).

Type Material: Holotype (Figures 1–4), ANSP 450580, from type locality, May 22, 1999; paratypes (Figures 5–6), ANSP 402244, 8 shells and Institute of Jamaica, 2 shells, from type locality; ANSP 403039, Jamaica, St. Andrew Parish, John Crow Peak, Blue Mountains, elfin forest with bamboo near summit, 18°05′45″ N, 76°40′08.4″ W, altitude 1755 m, May 22, 1999; sta. JBS4a, 16 shells; ANSP 403040, Jamaica, St. Andrew Parish, Vinegar Hill Trail near head of Clyde River, 18°05′ N, 76°39′18″ W, altitude 1520 m, May 22, 1999, sta. JBS 5, 3 shells.

Type Locality: Jamaica, St. Andrew Parish, John Crow Peak, Blue Mountains; litter sample collected at base of limestone cap, 18°5′50″ N, 76°40′5″ W, altitude 1550 m, May 22, 1999, sta. JBS4c.

Other Material Examined: Digital images of two specimens from Red Hills Road Cave, Jamaica (Paul and Donovan, 2005), Paul collection.

Etymology: The specific name *marciae* refers to Dr. Marcia Mundle, then of the Jamaica Conservation and Development Trust. Dr. Mundle arranged for the vehicle used and park ranger guide that accompanied the expedition to the type location, and was present when the species was first collected.

RESULTS AND DISCUSSION

Variation: *Vertigo marciae* is rather constant in general appearance in terms of its shape, color, sculpture, and development of the apertural lamellae. While some variation in size (especially height) was noted, this was minor—only 16% difference between the largest and smallest shells was observed.

Comparison with Other *Vertigo* Species: *Vertigo marciae* differs from all other *Vertigo* species by its small (<1.7 mm in height) yellow shell with indistinct striae/wrinkles, flared aperture base, and lack of angular and basal lamellae. It is closest in appearance to *V. hebardi* of the Florida Keys (Figure 7), with which it shares a small yellow shell, the lack of a basal lamella, and preference for accumulations of tropical forest leaf litter. However, it differs from this species in its taller shell with less distinct striae and absence of an angular lamella. It is also reminiscent of *Vertigo marki* Gulick,

Figures 1–12. Stereomicroscope images of *Vertigo marciae* and related taxa. **1–4.** *Vertigo marciae*, holotype, Jamaica, St. Andrew Parish, John Crow Peak, Blue Mountains, 18°5′45″ N, 76°40′8″ W to 18°5′50″ N, 76°40′5″ W, ANSP 450580. **1.** Apertural view. **2.** Profile. **3.** Umbilical view showing parietal and upper palatal lamellae. **4.** Apical view showing protochonch and the basal apertural dilation. **5.** *Vertigo marciae*, ANSP 402244, Paratype, second specimen from the type locality, exhibiting a shorter shell. **6.** *Vertigo marciae*, ANSP 402244, Paratype, third specimen from the type locality, exhibiting a slightly more worn shell. **7.** *Vertigo hebardi*, Long Key, Monroe County, Florida, 24°48′52″ N, 80°49′14″ W, JCN 17479. **8.** *Vertigo gouldii* (small southern form), Tellico Gorge, Monroe Co., Tennessee, 35°19′49″ N, 84°10′59″ W, BFC 1332. **9.** *Vertigo alabamensis*, Lanier Quarry, Pender Co., North Carolina, 34°37′49″ N, 77°40′27″ W, JCN 10781. **10.** *Vertigo "conecuhensis,"* Pond Creek seep, Covington Co., Alabama, 31°6′12″ N, 86°32′3″ W, JCN 12364. **11.** *Vertigo oscariana*, Wadboo Creek, Berkeley Co., South Carolina, 33°11′50″ N, 79°56′46″ W, JCN 10908. **12.** *Vertigo gouldii* (normal form), Deer Creek, Fillmore Co., Minnesota, 43°43′56″ N, 92°20′39″ W, JCN 14646.

1904 from Bermuda, with which it shares a smooth, yellowish shell that lack both basal and angular lamellae (Pilsbry, 1919). However, *V. marciae* differs from this species by its smaller shell height and lack of a callus on the palatal wall of the aperture. *Vertigo oscariana* from the southeastern USA (Figure 11) also has a small, smooth yellow shell without a basal lamella, but this species also lacks an upper palatal fold, has a callus on the outer apertural margin, and a shell that is widest in the middle, tapering both to base and apex. *Vertigo alabamensis* of the southeastern North American coastal plain (Figures 9, 10) also has a yellowish shell lacking striae, but this species is larger (generally >=1.8 mm tall), possessing both angular and basal lamellae, a strong crest on the apertural margin, and a strong sinulus on the palatal wall of the aperture.

Rosenberg and Muratov (2006) identified *Vertigo marciae* as *Vertigo gouldii* (Figures 8, 12) because of its general shell shape and placement of the parietal lamella and palatal folds, and also because *V. gouldii* was reported from Jamaica by Pilsbry and Cooke (1919: 99). However, *V. gouldii* has a larger shell of brown color, has a duller shell luster from the presence of abundant strong but irregular striae, and always possesses a basal lamella. Specimens documenting the Pilsbry and Cooke record have not been traced, and are apparently based on personal communication between Victor Sterki and Pilsbry. Bequaert and Miller (1973: 95) rejected Antillean records of *V. gouldii*.

While *Vertigo milium*—which also occurs in Jamacian tropical forest leaf litter—possesses a shell <1.7 mm tall; this species is easily distinguished from *V. marciae* in its dark red-brown color, presence of both angular and basal lamellae, and its long, curved lower palatal fold which deeply enters the shell.

Geographic Distribution and Ecology: *Vertigo marciae* is currently known in the Recent fauna only from the crest of John Crow Peak and its immediate vicinity in the Blue Mountains of eastern Jamaica at elevations of 1520–1755 m. John Crow Peak is capped by an isolated limestone outlier known to have distinctive plant communities, including endemic species (Grossman et al., 1993). (Note that John Crow Peak is not the same location as the John Crow Mountains, the easternmost range of Jamaica.) *Vertigo marciae* is found mainly on or adjacent to limestone boulders and outcrops in tropical as well as scrub forest with bamboo, but has also been found at one site (JBS 5) that lacks exposed limestone.

As a Pleistocene fossil, it is known only from Red Hills Road Cave, which is about 21 km west of Rosenberg and Muratov's sites on John Crow Peak and 1000 m lower in elevation (520 m, Paul and Donovan, 2005). *Vertigo marciae* joins the two *Radiodiscus* species and the *Punctum* reported by Paul and Donovan (2005) on the basis of personal communication from Rosenberg as species known in Jamaica only from John Crow Peak and from the Red Hills Road Cave. Paul and Donovan interpreted the faunal changes from the Red Hills Road Cave fauna to the recent fauna around the cave as suggesting drying of the climate since the Pleistocene. As *Vertigo marciae* was found nowhere else in Jamaica among the hundreds of sites sampled by Rosenberg and Muratov, its current occurrence might represent a relict distribution.

Although it must currently be considered a Jamaican endemic, the general lack of local endemism in the genus *Vertigo* (Nekola, 2009) suggests the possibility that it may occur elsewhere in the adjacent Caribbean, especially on carbonate substrates in mid- to high-elevation montane forest.

Table 2. Average number of base-pair differences between all pairwise combinations of *Vertigo marciae* and related species.

A. *CytB* amplicon (355 base pairs)				
V. oscariana	53.1			
V. alabamensis	65.6	54.3		
V. hebardi	62.3	52.0	8.3	
V. marciae	63.8	46.5	38.7	36.0
	V. gouldii	*V. oscariana*	*V. alabamensis*	*V. hebardi*
B. *16S* amplicon (443–447 base pairs)				
V. oscariana	40.9			
V. alabamensis	37.3	44.5		
V. hebardi	35.8	44.5	4.0	
V. marciae	42.5	42.0	18.0	18.0
	V. gouldii	*V. oscariana*	*V. alabamensis*	*V. hebardi*
C. Concatenated *ITS-1* and *ITS-2* amplicons (1274–1284 base pairs)				
V. oscariana	34.8			
V. alabamensis	32.3	20.5		
V. hebardi	34.3	22.5	5.0	
V. marciae	37.3	23.5	9.0	12.0
	V. gouldii	*V. oscariana*	*V. alabamensis*	*V. hebardi*

Genetic Distinctness and Phylogenetic Relationships: DNA sequence analysis clearly demonstrates that *V. marciae* is distinct at the species level. It possesses an average of 36 and 39 base pair differences with *V. hebardi* and *V. alabamensis*, respectively, in the 355 bp *CytB* amplicon (Table 2). This equates to a 10–11% variation across the entire amplicon. In addition, it possessed an average of 46.5 base pair differences in *CytB* (13%) with *V. oscariana* and 63.8 differences (18%) with *V. gouldii*. In the more slowly evolving 443 to 447 bp *16S* region *V. marciae* differed by 18 bases (4.0%) from *V. hebardi* and *V. alabamensis*, 42 bases (9.4%) from *V. oscariana*, and 42.5 bases (9.6%) from *V. gouldii*. In the concatenated 1274–1284 bp *ITS-1* + *ITS-2* nDNA amplicon, *V. marciae* possessed an average of 9 base-pair (0.7%) differences with *V. alabamensis*, 12 (0.9%) with *V. hebardi*, 23.5 (1.8%) with *V. oscariana*, and 37.3 (2.9%) with *V. gouldii*. These levels of difference were considerably larger than those exhibited between the conchologically distinct *V. alabamensis* and *V. hebardi* (Figures 7, 9, 10), which amounted to an average difference of 8.3 bases (2.3%) in *CytB*, 4.0 (0.9%) in *16S*, and 5.0 (0.4%) in concatenated *ITS-1* and *ITS-2*.

The topologies across phylogenetic reconstructions were largely compatible, with the same highly supported nodes being identified in all cases (Figures 13–15). These demonstrate that *V. marciae* is clearly a member of the genus *Vertigo*, being within the same highly supported clade in *CytB* and *16S* that includes *V. pusilla*, the type species of the genus. While it was not possible to root the concatenated *ITS-1* + *ITS-2* tree because of profound differences with both *Gastrocopta cristata* and *Pupilla muscorum* sequences, *V. marciae* was easily aligned with all *Vertigo* sequences.

The phylogenetic reconstructions also demonstrate that *V. marciae* is a member of a highly supported clade that includes both *V. alabamensis* and *V. hebardi*. The existence of a single ancestor to all of these species implies long distance dispersal from the southeastern United States to Jamaica, perhaps with migrating birds as a vector. This is not an unreasonable scenario, given that much longer feats of long distance dispersal via migrating birds have been documented in the eastern Atlantic (Gittenberger et al., 2006).

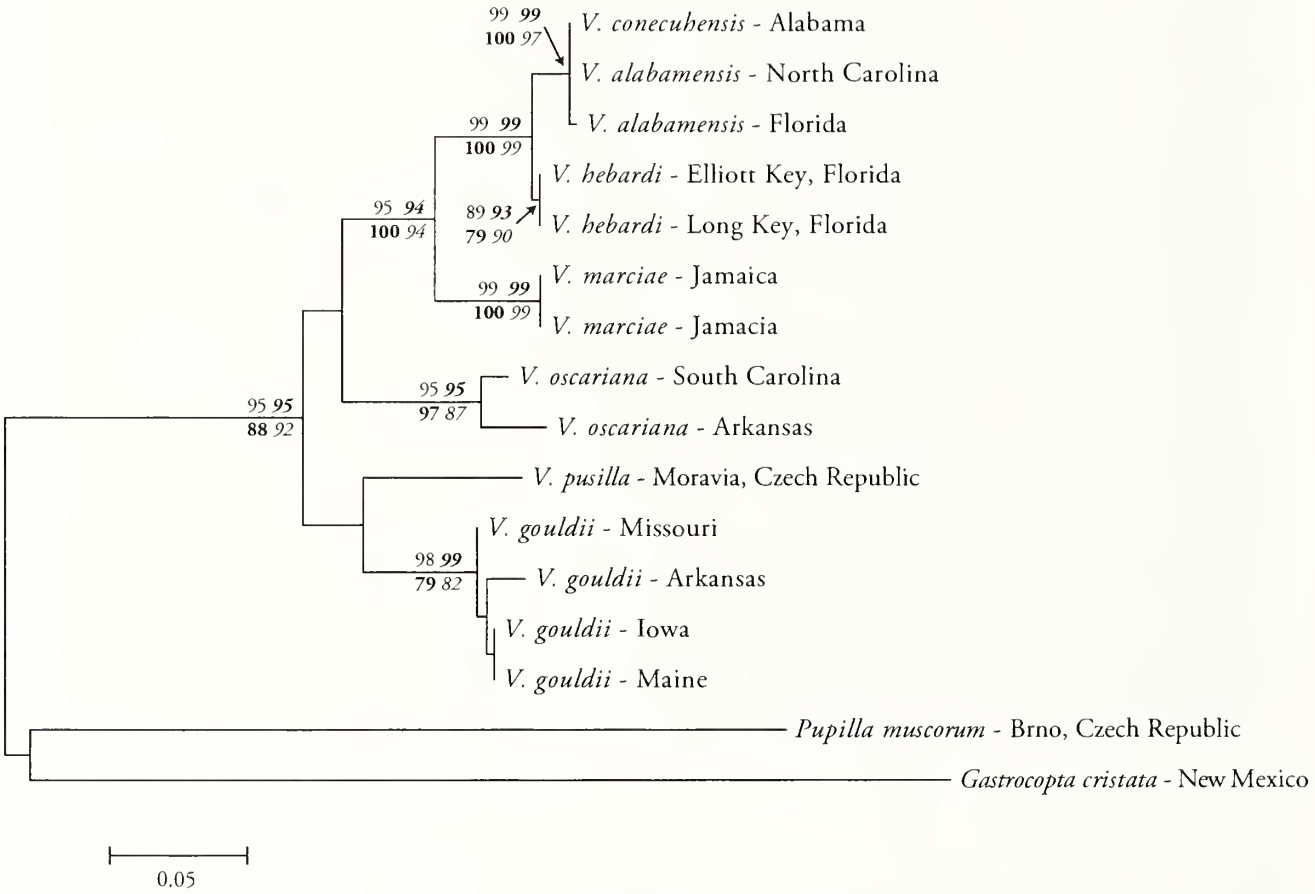

Figure 13. The phylogenetic relationships of *Vertigo marciae* as reconstructed by maximum-likelihood analysis from the *CytB* amplicon. Nodes with strong to moderate support across all four phylogenetic reconstruction methods have been labeled to the left of that node by four support values: The upper left (normal font) is for nearest neighbor joining. The upper right (***bold italic font***) is for maximum parsimony. The lower left (**bold font**) is for Bayesian. The lower right (*italic font*) is for maximum likelihood.

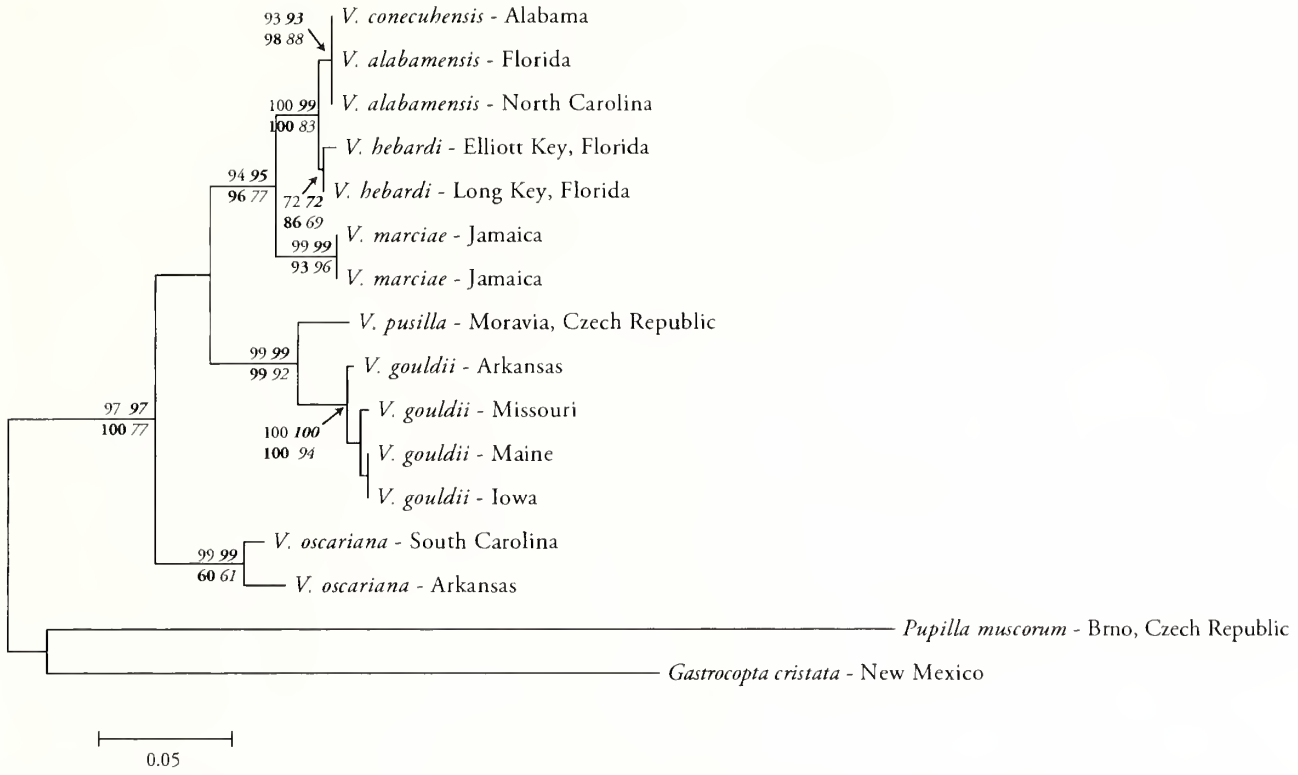

Figure 14. The phylogenetic relationships of *Vertigo marciae* as reconstructed by maximum-likelihood analysis from the *16S* amplicon. Nodes with strong to moderate support across all four phylogenetic reconstruction methods have been labeled to the left of that node by four support values: The upper left (normal font) is for nearest neighbor joining. The upper right (***bold italic font***) is for maximum parsimony. The lower left (**bold font**) is for Bayesian. The lower right (*italic font*) is for maximum likelihood.

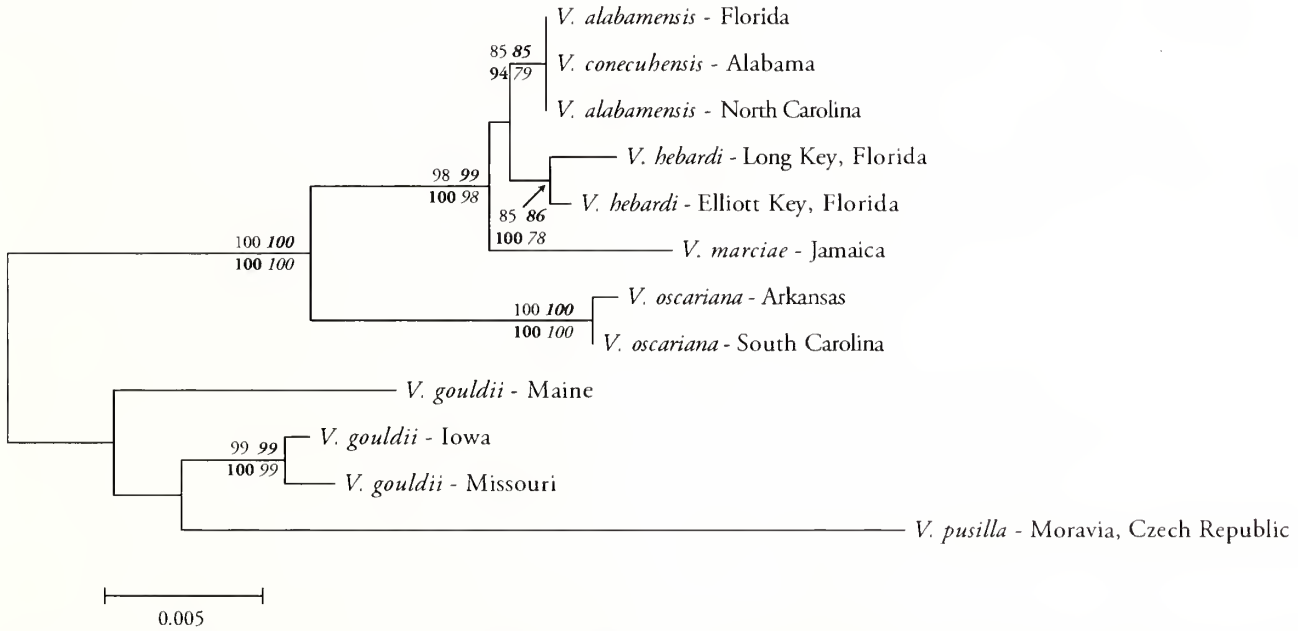

Figure 15. The phylogenetic relationships of *Vertigo marciae* as reconstructed by maximum-likelihood analysis from the concatenation of the ITS-1 and ITS-2 amplicons. Nodes with strong to moderate support across all four phylogenetic reconstruction methods have been labeled to the left of that node by four support values: The upper left (normal font) is for nearest neighbor joining. The upper right (***bold italic font***) is for maximum parsimony. The lower left (**bold font**) is for Bayesian. The lower right (*italic font*) is for maximum likelihood.

While resolution of deeper nodes within the genus *Vertigo* was not possible in the *CytB* and *16S* mtDNA amplicons (Figures 13, 14), presumably due to base-pair saturation, the concatenated *ITS-1+ ITS-2* data (Figure 15) demonstrated a very highly supported node connecting the *V. marciae* / *V. hebardi* / *V. alabamensis* clade to *V. oscariana*. This radiation includes some of the most distinct members of the genus (Pilsbry, 1948). Additional field work across the Caribbean—especially in Cuba, Hispaniola, Puerto Rico, and Bermuda—will be required to determine the actual number of species contained within this group.

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John Slapcinsky of the Florida Museum of Natural History provided ethanol-preserved tissue samples of *Vertigo hebardi*, while Michal Horsak of Masaryk University in Brno, the Czech Republic, provided live samples for *Vertigo pusilla* and *Pupilla muscorum*. *CytB* and *16S* sequences for *V. pusilla*, *P. muscorum*, and *Gastrocopta cristata* were retrieved from full mitochondrial genomic sequences provided by Jason Marquardt and Ulfar Bergthorsson of the University of New Mexico. Christopher Paul, University of Bristol, provided digital images of the Red Hills Road Cave fossils. Field work which established the persistence of *Vertigo hebardi* in the Florida Keys was supported by The Bailey-Matthews Shell Museum through an R.T. Abbott Visiting Curatorship to JCN. Additional funding for PCR and sequencing analysis was provided by Michal Horsak. The field work which resulted in the Recent samples of the new species being collected was supported by NSF Grant DEB-9870233 to Gary Rosenberg.

LITERATURE CITED

Bequaert, J.C. and W.B. Miller. 1973. The Mollusks of the Arid Southwest. University of Arizona, Tucson, xvi+271 pp.

Gittenberger, E., D.S.J. Groenenberg, B. Kokshoorn and R.C. Preece. 2006. Molecular trails from hitch-hiking snails. Nature 439: 409.

Grossman, D.H., S. Iremonger, and D.M. Muchoney. 1993. Jamaica: map of natural communities and modified vegetation types. Jamaica: a rapid ecological assessment. Phase 1: An island-wide characterization of mapping of natural communities and modified vegetation types. The Nature Conservancy, Washington, D.C., USA.

Huelsenbeck, J.P. and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17: 754–755.

Nekola, J.C. and B.F. Coles. 2010. Pupillid land snails of eastern North America. American Malacological Bulletin 28: 29–57.

Nekola, J.C. 2009. Big ranges from small packages: North American vertiginids more widespread than thought. The Tentacle 17: 26–27.

Nekola, J.C., B.F. Coles, and U. Bergthorsson. 2009. Evolutionary pattern and process in the *Vertigo gouldii* (Mollusca: Pulmonata, Pupillidae) group of minute North American land snails. Molecular Phylogenetics and Evolution 53: 1010–1024.

Paul, C.R.C. and S.K. Donovan. 2005. Quaternary and Recent land snails (Mollusca: Gastropoda) from Red Hills Road Cave, Jamaica Bulletin of the Mizunami Fossil Museum 32: 109–144.

Pilsbry, H.A. 1919. American Species of *Vertigo*. Manual of Conchology. Second Series (Pulmonata) 25: 74–150, pls. 6–13.

Pilsbry, H.A. 1948. Land Mollusca of North America (North of Mexico). Academy of Natural Sciences of Philadelphia Monographs 3, vol. 2(2): i–xlvii, 521–1113.

Rosenberg, G. and I.V. Muratov. 2006. Status report on the terrestrial mollusca of Jamaica. Proceedings of the Academy of Natural Sciences of Philadelphia 155: 117–161.

Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei, and S. Kumar. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular Biology and Evolution 28: 2731–2739.

Cornisepta guzmani new species: first species of genus confirmed from Pacific cold seep environments off central Chile (Gastropoda: Vetigastropoda: Fissurellidae)

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ABSTRACT

The new bathyal gastropod species, *Cornisepta guzmani* new species, collected at a depth of 846 metres from a methane seepage site in the subduction zone off Concepción (36°22′ S; 73°43′ W), central Chile, is described. The new species is most similar to *Cornisepta pacifica* (Cowan, 1969), described from offshore Alaska and Oregon, from which it differs in shell morphology, sculpture, and geographic distribution.

Additional Keywords: Deep water, deep sea

INTRODUCTION

The genus *Cornisepta* was established to group a series of small, deep-water fissurellids with high conical shells, lacking a selenizone, with a prominent internal septum, and that shed the protoconch as they age (McLean and Geiger, 1998). The genus comprises thirteen extant worldwide species, of which seven have been described from the Pacific Ocean: *Cornisepta antarctica* (Egorova, 1972), *C. festiva* (Crozier, 1966), *C. levinae* McLean and Geiger, 1998, *C. monsfuji* Chino, 2009, *C. pacifica* (Cowan, 1969), *C. soyoae* (Habe, 1951) and *C. verenae* McLean and Geiger, 1998. The genus has records up to the early Oligocene, with two species described for the early Rupelian of Germany; *Cornisepta anhaltina* Müller, 2011 and *C. granulocostata* Müller, 2011 (Müller, 2011). Recent species of *Cornisepta* have been recorded in deep-sea environments, in faunal associations of seamounts (Beck et al., 2006), in reducing systems at hydrothermal vents in mid-oceanic ridges (Sasaki et al., 2010), and cold seeps at continental margins (Gracia et al., 2011). Little is known of their population biology, ecology and conservation status.

This article describes *Cornisepta guzmani* based on shell morphology and sculpture of two specimens collected in methane-hydrate rubble and inside the valves of a vesicomyid clam collected in a methane cold seep off Concepción Bay, central Chile. In addition, external morphology and details of sculpture were compared with that of congeneric species in the Pacific Ocean and a species from the Atlantic Ocean.

MATERIALS AND METHODS

The description of the new species is based on two specimens collected from rubble trawled from a methane cold seep off the coast of Concepción Bay, central Chile (36° 22′ S; 73° 43′ W). The holotype and paratype are deposited under accession number 2013-001 in the collections of the Santa Barbara Museum of Natural History, Santa Barbara, California, USA (SBMNH).

For the morphological descriptions, the length (L), height (H) and width (W) of the shells were measured from photographs and scanning electron micrographs. The position of the foramen (PF) was defined as the distance of the centre of the foramen measured from the anterior shell margin.

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Suborder Vetigastropoda Salvini-Plawen, 1980
Family Fissurellidae Fleming, 1822
Subfamily Emarginulinae Children, 1834

Genus *Cornisepta* McLean and Geiger, 1998

Type Species: *Fissurisepta antarctica* Egorova, 1972 (by original designation), Recent, Weddell Sea, Antarctica (McLean and Geiger, 1998: 18).

Remarks: Chino (2009) and Müller (2011) erroneously attributed the genus name to McLean alone.

***Cornisepta guzmani* new species**
(Figures 1–7)

Diagnosis: Small fissurellid (up to 5.3 mm), conical profile, foramen at summit of shell, anterior slope convex, posterior slope concave, septum high, across, thin, sculpture of widely spaced pustules randomly hyperdispersed.

Description: Shell of moderate size for genus, yellowish-white, conical, anterior slope convex, profile moderately high (66% of length), posterior slope concave. Juvenile shell and protoconch unknown. Foramen oval, situated in posterior third of shell length. Sculpture of concentric growth marks with widely spaced pustules arranged randomly hyperdispersed. Interior of shell glossy, septum thin, slightly curved, transverse, extending obliquely downward at an angle of approximately 42° from the anterior slope for almost half the height of the shell. Outline of peristome flat.

Type Material: Holotype SBMNH 236523, 5.26 × 3.77 × 3.47 mm (L×W×H); paratype SBMNH 236524, 2.66 × 1.71 × 1.55 mm (L×W×H).

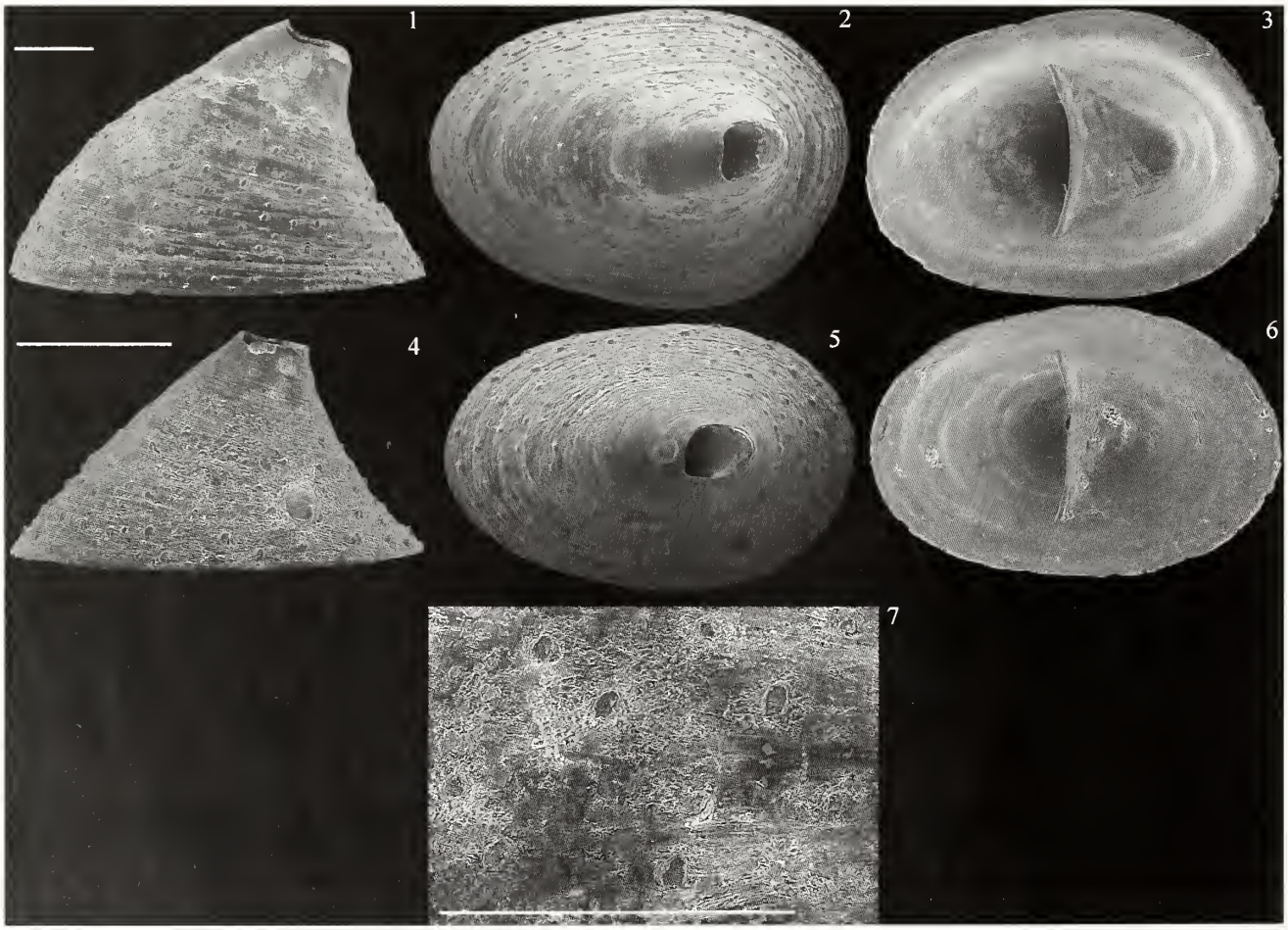
Type Locality: Concepción Bay methane seep area, off Concepción, Chile, Southeast Pacific Ocean, RV Agor Vidal Gormáz, 36° 22′ S; 73° 43′ W, 846 m depth, coll. & leg. Guillermo Guzmán.

Etymology: Named in honor of Guillermo Guzmán, Museo del Mar, Universidad Arturo Prat, Iquique, Chile, who donated the type material of this new species.

Remarks: This species lives in or near methane hydrate rubble. The holotype had a portion of the body remaining in the shell, although the head with radula unfortunately was not available.

DISCUSSION

Seven species assigned to the genus *Cornisepta* have been recorded in the Pacific Ocean; *C. acuminata*



Figures 1–7. *Cornisepta guzmani* new species. **1.** Holotype SBMNH 236523, 5.26 mm, lateral view. **2.** Holotype, dorsal view. **3.** Holotype ventral view. **4.** Paratype SBMNH 236524, 2.66 mm, lateral view. **5.** Paratype, dorsal view. **6.** Paratype, ventral view. **7.** Paratype, detail of sculpture. Scale bars = 1 mm.

Table 1. Summary of shell characters of *Cornisepta* species from the Pacific Ocean based on Chino (2009), Cowan (1969), McLean and Geiger (1998), and this study. PF: position of foramen.

Species	H	W	L	(H/L)	Profile anterior side	Profile posterior side	Shell sculpture	PF
C. acuminata	4.0	3.5	5.0	0.8	Straight	Slightly concave	Dense, round pustules	0.74
C. antarctica	6.7	4.9	7.0	0.96	Straight to slightly concave	Straight to slightly concave	T-shaped pustules	0.61
C. festiva	5.9	-	5.2	1.13	Convex to slightly straight	Slightly concave	Very tenuous pustules	0.66
C. levinae	3.5	4.1	5.2	0.67	Slightly convex	Slightly concave	Thin, elongate pustules	0.56
C. monsfuji	2.2	1.4	2.1	1.05	Convex	Slightly concave	Axial ordered minute pustules	0.61
C. pacifica	3.6	3.5	4.8	0.75	Convex	Slightly straight	Few small pustules in horizontal rows	0.66
C. soyoae	2.3	2.4	3.6	0.64	Convex	Concave	Pustules in rows arranged obliquely	0.61
C. verenae	1.3	1.3	1.6	0.81	Convex	Concave	Pustules linked in chains	0.56
C. guzmani n. sp.	3.5	3.8	5.3	0.62	Convex	Concave	Pustules widely separated	0.73

Watson, 1883 from the Western Atlantic (290–710 m) is also included (Table 1); *C. antarctica* from the Weddell sea, Antarctica, in 280–700 m depth and the Bellinghausen Sea, Antarctica in a depth range of 400–500 m (Aldea et al., 2008), *C. festiva* from northwest of the Three Kings Islands, New Zealand, in 805 m, *C. levinae* from the summit of Volcano 6, Eastern Pacific Rise (12° 44′ N, 102° 33′ W) in 1775 m depth, *C. monsfuji* from the SE China Sea, southwestern Japan in 240–270 m, and from off Olango Island, Philippines, in 60 m, *C. pacifica* from Kiska, Aleutian Islands, Alaska to southern California, in a depth range of 440–880 m (McLean and Geiger, 1998), *C. soyoae* from Sagami Bay, Japan in 120–170 m depth and *C. verenae* from Axial Seamount, Juan de Fuca Ridge (45° 56′ S, 130° 04′ W) in 1530 m depth. All of the species have shelf to bathyal distributions, and two of them (*C. levinae* and *C. verenae*) occur only at hydrothermal vents (McLean and Geiger, 1998; Sasaki et al., 2010).

Cornisepta guzmani has a shell similar to *C. pacifica*; the new species differs in having a lower profile (66 vs. 76% L/H), a more concave posterior profile, a larger angle between the septum and the anterior slope and sparse pustules over the shell. Moreover, *C. guzmani* has been found at cold seeps while *C. pacifica* has not been associated with such habitats. *Cornisepta antarctica* and *C. festiva* differ from the new species in their larger shells with height almost equal or even greater than length (96%, 113% L/H, respectively), have different sculpture of pustules (with t-shaped pustules in *C. antarctica*) that are more delicate than in *C. guzmani*, and straighter anterior and posterior profiles. *Cornisepta levinae* and *C. verenae* differ from *C. guzmani* in the higher profile (67%, 81% L/H, respectively), the more densely ornamented shell, and the comparatively smaller and more neatly ordered pustules, with *C. verenae* exhibiting a distinct sculpture of chained pustules encircling the shell. *Cornisepta monsfuji* and *C. soyoae* differ from the new species in having smaller shells, higher profiles (*C. monsfuji* has a taller than wider shell), and more strongly ornamented shells, with pustules aligned in vertical rows in *C. monsfuji* and in oblique prosocline rows in *C. soyoae*. They also have bathymetry ranges shallower than *C. guzmani*. *Cornisepta acuminata* has much denser pustules and a much taller shell.

So far, *C. guzmani* has the lowest shell profile, with the most posteriorly placed foramen of all the Pacific *Cornisepta* species. It is also the second species to be recognized living at a cold seep, after *C. acuminata* (Watson, 1883), reported for the Sinu River delta methane seep (09° 02′ N, 76° 02′ W), Colombia in 500 m depth (Gracia et al., 2011), and the first such fissurellid species for Chile and the southeastern Pacific coast.

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Guillermo Guzmán, Museo del Mar, Universidad Arturo Prat, Chile, who collected the first specimen of the new species. Arnold Müller, Leipzig University, Germany, Dai Herbert, KwaZulu-Natal Museum, South Africa, and Lindsey Groves, Los Angeles County Museum of Natural History, California, USA, provided literature and commented on the genus. Bruce Marshall, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand and an anonymous reviewer critically reviewed the manuscript.

LITERATURE CITED

Aldea, C., C. Olabarria, and J. Troncoso. 2008. Bathymetric zonation and diversity gradient of gastropods and bivalves in West Antarctica from the South Shetland Islands to the Bellingshausen Sea. Deep-Sea Research Part I: Oceanographic Research Papers 55(3): 350–368. http://dx.doi.org/10.1016/j.dsr.2007.12.002

Beck, T., T. Metzger, and A. Freiwald. 2006. BIAS – Biodiversity inventorial atlas of macrobenthic seamount animals. OASIS Deliverable 25 Final Report: 1–124.

Chino, M. 2009. A new species of the genus *Cornisepta* McLean, 1998 [sic] (Gastropoda: Fissurellidae) from Japan. Venus 68: 63–66.

Cowan, I.M. 1969. A new species of gastropod (Fissurellidae, *Fissurisepta*) from the eastern North Pacific Ocean. The Veliger 12: 24–26.

Crozier, M.A. 1966. New species and records of Mollusca from off Three Kings Islands, New Zealand. Transactions of the Royal Society of New Zealand, Zoology 8: 39–49.

Gracia, A., N. Rangel-Buitrago, and J. Sellanes. 2011. Methane seep molluscs from the Sinu-San Jacinto fold belt in the Caribbean Sea of Colombia. Journal of the Marine Biological Association of the United Kingdom 92: 1367–1377. doi: 10.1017/S0025315411001421

Habe, T. 1951. Fissurellidae in Japan. Illustrated catalogue of the shells of Japan 17: 109–120, pl. 17.

Habe, T. 1964. Shells of the Western Pacific in color, Vol. II. Osaka: Hoikusha, 233 pp., 66 pls.

McLean, J.H. and D.L. Geiger. 1998. New genera and species having the *Fissurisepta* shell form, with a generic-level phylogenetic analysis (Gastropoda: Fissurellidae). Contributions in Science, Natural History Museum of Los Angeles County 475: 1–32.

Müller, A. 2011. First record of fossil *Cornisepta* McLean 1998 [sic] from the North Sea Basin (Early Oligocene, Central Germany) (Gastropoda Vetigastropoda: Fissurellidae). Archiv für Molluskenkunde: International Journal of Malacology, 140: 239–244.

Sasaki, T., A. Warén, Y. Kano, T. Okutani, and K. Fujikura. 2010. Gastropods from Recent hot vents and cold seeps: systematic, morphology and life strategies. Topics in Geobiology 33: 169–254.

A new species of *Lithasia* (Gastropoda: Pleuroceridae) from the Buffalo River, Tennessee, USA

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ABSTRACT

A new species of pleurocerid snail, *Lithasia bubala* new species, is described from the Buffalo River, Tennessee, USA. The species is sister to *Lithasia geniculata* from the Duck River in Tennessee, and can be separated from it both morphologically and using mitochondrial DNA sequences. *Lithasia bubala* represents the first snail endemic to the Buffalo River watershed.

Additional Keywords: Lithasia geniculata, Duck River, COI sequences

INTRODUCTION

Pleuroceridae is a family of gill-breathing, operculate snails found in North America that reaches its greatest diversity in the southeastern United States (Burch and Tottenham, 1980; Lydeard and Mayden, 1995; Lydeard et al., 1997; Strong and Frest, 2007). Stabilizing the taxonomy of pleurocerids in general is desirable given the state of freshwater mollusks taxonomy in North America. Like many other non-marine invertebrate groups (Lydeard et al., 2004), pleurocerids are experiencing declines in the number of species and individuals because of anthropogenic activities (Bogan et al., 1995; Lydeard et al., 1997), and because taxa with small geographical ranges tend to be more highly imperiled (Jablonsky, 1982). For example, in the Mobile Basin, all species in one genus (*Gyrotoma*) and approximately 31 species of other genera are presumed extinct (Bogan et al., 1995). Recent efforts have improved our understanding of the family and its systematics (Lee et al., 2006; Dillon and Robinson, 2009; Strong and Köhler, 2009), though more work is needed in terms of species delineation and conservation (Perez and Minton, 2008).

The genus *Lithasia* is one of six extant genera in Pleuroceridae. The majority of work treating the genus is concentrated on the taxonomy (based on shell characters) and synonymy of the nominal species that comprise the modern *Lithasia* (Tryon, 1873; Goodrich, 1940; Burch and Tottenham, 1980) using shell characters. One group in need of revision includes those individuals currently recognized as *Lithasia geniculata* Haldeman, 1840. In modern treatments (e.g. Burch, 1982), *L. geniculata* is comprised of three subspecies, *geniculata*, *fuliginosa* (Lea, 1841), and *pinguis* (Lea, 1852), occurring in the Cumberland and Duck River drainages in Kentucky and Tennessee. Each subspecies was originally described as its own species (Tryon, 1873) and later synonymized. Differences between taxa were based on conchological features and where they occurred within a river system. *Lithasia g. pinguis* was considered the headwaters form, transitioning into the *L. g. fuliginosa* form mid-river, then into the *L. g. geniculata* form in the deeper main stem. Minton and Lydeard (2003) suggested that *L. geniculata* represented multiple species based on analyses of morphology and mitochondrial COI DNA sequences, while Minton et al. (2008) showed that much of the shell variation in this group was due to phenotypic plasticity. This paper aims to clarify the taxonomy of *L. geniculata* by describing a new species from within the species' putative range.

MATERIALS AND METHODS

Specimens of the new species described here were found in the collections of the Florida Museum of Natural History, Gainesville, Florida (FLMNH), Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ), and the Museum of Zoology, Ann Arbor, Michigan (UMMZ). Vouchers were deposited at the North Carolina Museum of Natural Sciences, Raleigh, North Carolina (NCMS) and the University of Alabama gastropod collection, Tuscaloosa, Alabama (UAG). Taxonomy follows Turgeon et al. (1998; but see Dillon, 2011). Radulae were prepared according to Holznagel (1998) and visualized on a Hitachi S2500 scanning electron microscope. The distribution map was generated in DIVA-GIS 7.1.6 (Hijmans, 2009).

Cytochrome oxidase subunit I sequences from Minton and Lydeard (2003) were combined with selected

non-*Lithasia* sequences from Sides (2005) and an unpublished *Juga orickensis* sequence from GenBank (Appendix 1) as the outgroup. Eight additional sequences from the new species were generated by the author and were identical to those generated previously (AF435747-8). All sequences were aligned by eye and analyzed under maximum likelihood using the CIPRES 2.0 version of RA×ML 7.2.5 (Stamatakis et al., 2008) under the GTR+I+G model as suggested by jModelTest (Posada, 2008). Branch support was assessed using 100 non-parametric bootstrap replicates in RA×ML. To determine the degree of exclusive ancestry (i.e. complete lineage divergence), the genealogical sorting index (*gsi*; Cummings et al., 2008) was calculated using 10,000 replicate generations. Values for *gsi* range from zero to one, with one indicating monophyly and complete separation from other lineages; a p-value indicates significance of the *gsi*. To date the divergence of clades from one another, BEAST 1.54 (Drummond and Rambaut, 2007) was used to estimate times to most recent common ancestors (TMRCA) for *Lithasia geniculata*. The GTR+I+G model was used and anchored with the estimated pleurocerid-semisulcospirid split at 90 MYA (Strong and Köhler, 2009). A Yule process tree prior was used for comparing different species with an uncorrelated log-normal relaxed clock hypothesis to allow for rate heterogeneity in the tree (Drummond et al., 2006). The analysis ran for ten million states, logging every ten thousandth state. BEAST results were visualized in Tracer 1.5 (Rambaut and Drummond, 2009) and recorded as mean time ± standard error.

RESULTS

Maximum likelihood analysis yielded a single tree (−6178.75, α=1.24, pinvar=0.55) with well-supported relationships between species of *Lithasia* (Figure 1). Snails identified as *L. geniculata* from the "Cumberland"

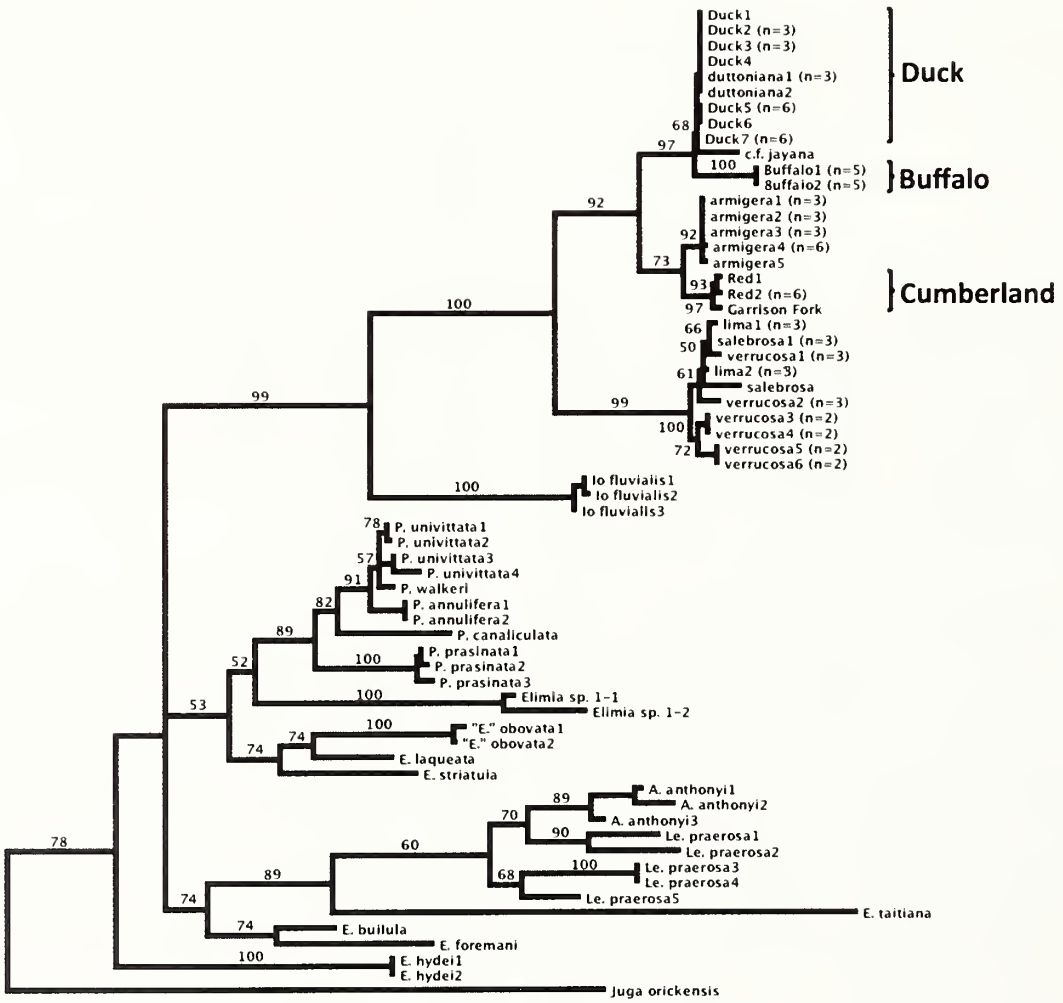

Figure 1. Maximum likelihood tree showing relationships of *Lithasia geniculata* populations to other pleurocerids. One individual was sequenced unless otherwise noted. Values above branches are non-parametric bootstrap values >50%.

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          1233334447899999111111222333444444445555555666666677777888888888
           8257936802456781256693561480113489991577899001127903466011355557 8
                               8143692720089123510591047648130680636703834845697 0
Buf        TCACACTTTGCTACTAGCAATCCCGGTTTTGTACCTACCTTCGTGGCCAAATTTGAAGTCAGTTGA
Duck1      ............................GT...T.....C.TA.T..C.T..GA..TA.GTA.AT
Duck2      ......................T......GT...T.....C.TG.T..C.T..GA..TA.GTA.AT
Jay        .TA.TTCGG..ACTAC.............GT...T.....C.TG.T..C.T..GA..TA.GTA.AT
GarFk      .T.T.....AT.....ATGGCT.TAACCCGTCGTT.G.TCCTTGTTTTCGTCCG.GTTATGTAC.T
Red1       .T.T.....AT.....ATGGCT..AACCCGT.GTTGG.TC.TTGTTTTCGTCCG.GTTATGTAC.T
Red2       AT.T.....AT.....ATGGCT.TAACCCGT.GTT.G.TCCTTGTTTTCGTCCG.GTTATGTAC.T
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Figure 2. Nucleotide substitution patterns for nominal *Lithasia* species from Tennessee used in this study. The single haplotype found in the Buffalo River is used for reference. Position numbers (based on 890 bp sequence) are above the nucleotides. Duck1 and 2 represent two haplotypes shared by *L. duttoniana* and *L. geniculata* from the Duck River. Red1 and Red2 represent two haplotypes shared by *L. geniculata* from the Red River. The single specimen of *L. cf. jayana* from the Duck River possessed a unique haplotype (Jay), as did the single *L. geniculata* from Garrison Fork (GarFk). Complete locality information can be found in Minton and Lydeard (2003).

(Red River plus Garrison Fork), Duck, and Buffalo drainages each formed reciprocally monophyletic clades; 'Cumberland' samples were sister to *L. armigera*, while Duck and Buffalo samples were sister to one another. All individuals from the Buffalo River shared a single unique haplotype (Figure 2). Analysis using *gsi* showed that each clade is genealogically separate from the others (*gsi* = 0.91–0.99, $p \ll 0.001$). The TMRCA for Duck and Buffalo River *Lithasia* was dated at 4 million ± 28,000 years ago, with the new species coalescing at 274,000 ± 5,000 years ago.

SYSTEMATICS

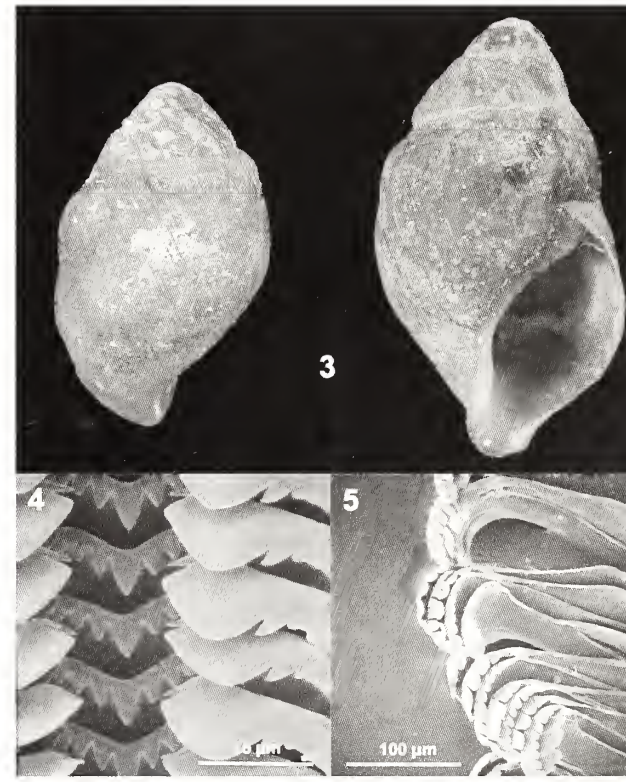
Class Gastropoda Cuvier, 1791
Family Pleuroceridae Fischer, 1885

Genus *Lithasia* Haldeman, 1840

Lithasia bubala new species
Buffalo Rocksnail
(Figures 2–6)

Diagnosis: Large shell compared to sympatric pleurocerids, ovately conic, golden-brown in color, frequently with posterior tubercles on body whorl, and posterior callus on columella. Body reddish-orange with black mottling. All sequenced individuals to date possess a single unique COI mitotype (Figure 2).

Description: Shell large, thick, ovately conic, height to 40 mm (Figure 3). Spire short and tapered, often eroded. Body whorl smooth, often plicate toward the suture, varying frequently with angular ridge on lower half. Transverse growth lines apparent. Sutures partially impressed, but regular and distinct. Aperture fusiform, one-half shell length. Columella white, with thick anterior and posterior calluses on parietal wall. Shell golden brown, frequently with purple-brown bands. Animal reddish-orange mottled with black. Tentacles bluish, wider at base, shorter than snout length. Radular rachidian tooth with nine triangular cusps, central cusp broader and longer than others (Figure 4). Lateral tooth broad, top concave, with three cusps. Interior cusp sharp and narrow. Central cusp large, broad, and lanceolate. External cusp short, pointed, incurved, one-fifth length of central cusp (Figure 4). Inner marginal teeth with six to eight denticles of equal size except for outer denticle on each side. Outer marginal teeth with



Figures 3–5. 3. *Lithasia bubala* new species holotype FMNH 297357. 16.9 mm. **4.** *Lithasia bubala* new species rachidian and lateral teeth. **5.** *Lithasia bubala* new species marginal teeth.

11 to 13 denticles, of equal size except for outer denticle on each side (Figure 5).

Type Locality: Buffalo River at takeout for Heath's Canoe Rental, 1076 Highway 13 N, Lobelville, Perry County, Tennessee, USA. Approximate coordinates: 35.772° N 87.784° W.

Type Material: Holotype FMNH 297357; Paratypes UAG 395.

Other Material Examined (all from Buffalo River, Tennessee): ANSP 178961, north of Riverside, Lewis County; FLMNH 35957, 12 miles north of Waynesboro, Wayne County; FLMNH 82131, above Linden, Perry County; FLMNH 82169, 5 mi. N of Lobelville, Perry County; FLMNH 82182, Beardstown, Perry County; FLMNH 232610, 1.1 miles north of Napier, Lewis County; FLMNH 232615, 0.7 mi. NW of Flat Woods, Perry County; FLMNH 232616, 2.0 mi. SSW of Lobelville, Perry County; MCZ 93695, above Linden, Perry County; MCZ 93701, 5 mi. N of Lobelville, Perry County; MCZ 93711, Beardstown, Perry County; UAG 406, Buffalo River Camping and Canoeing, 0.7 miles from Highway 13, south of Interstate 40, Humphreys County; UMMZ 53215, 5 mi. N of Lobelville, Perry County; UMMZ 53216, 5 mi. N of Lobelville, Perry County; UMMZ 53219, Beardstown, Perry County; UMMZ 53224, above Linden, Perry County; UMMZ 53225, Topsy Bridge, Wayne County; UMMZ 63873, 0.5 miles above mouth, Humphreys County; UMMZ 154173, north of Riverside, Lewis County; UMMZ 154174, 7 mi. S of Linden, Perry County.

Comparison with Duck River *L. geniculata*: Given their reciprocal monophyly, body color is the easiest way to distinguish between the two species. In addition, there is no overlap in their geographic ranges. In life, individuals of *L. bubala* had orange-red bodies, while the Duck River *L. duttoniana*, *L. geniculata*, and *L. jayana* used in this study had greenish-yellow bodies. While useful in this distinction, no study has documented variations in body color in pleurocerids, so its systematic utility remains unknown. Also, the tentacles of *L. bubala* tend to be darker blue-green and wider at the base than those of *L. geniculata*. Again, the systematic utility of tentacle characters remains unknown.

Etymology: From Latin *bubalus*, an antelope, buffalo, or ox, in reference to its endemism in the Buffalo River.

Distribution: Limited to the Buffalo River, Tennessee (Figure 6).

DISCUSSION

The analysis of Minton and Lydeard (2003) suggested that *Lithasia geniculata* from the Buffalo River, Tennessee, represented a species separate from individuals from the Duck River. Eight additional sequences and subsequent analysis confirmed this finding and highlighted the need to describe Buffalo River *L. geniculata* as a unique species. The delineation of *Lithasia bubala* satisfies multiple species concepts with its diagnostic body color compared to sister species (morphological), monophyly (phylogenetic [Baum and Donoghue, 1995]), and complete genealogical separation as measured by *gsi* (genealogical [Avise and Ball, 1990]). Taken together, *L. bubala* additionally satisfies the criteria for the encompassing, non-diagnostic evolutionary (Wiley and Mayden, 2000) and unified (de Queiroz, 2005) species concepts.

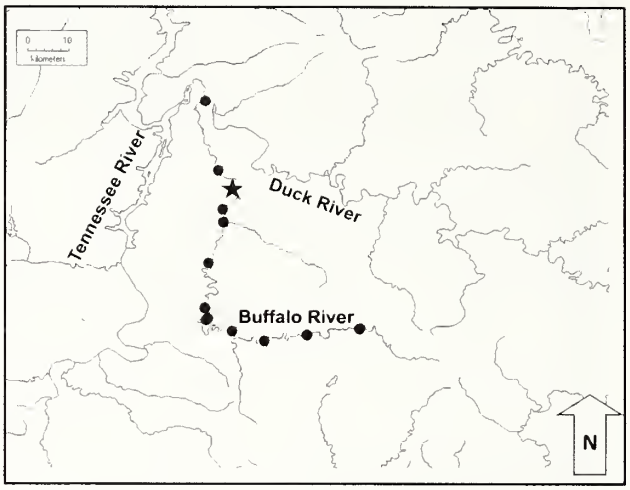


Figure 6. Distribution map of *Lithasia bubala* in the Buffalo River based on museum collections. Type locality is indicated with a star.

The sister relationship of *Lithasia bubala* to all Duck River *Lithasia* (*L. duttoniana*, *L. geniculata*, and *L. jayana*) was not entirely unexpected, as the relationship was shown previously (Minton and Lydeard, 2003), and given that the Buffalo River is the largest tributary to the Duck River. Additionally, the two rivers partially share freshwater faunal assemblages (Ortmann, 1924; van der Schalie, 1973). The Red River and Garrison Fork grouping supports the notion that fauna from the Upper Duck drainage has a Cumberlandian origin (van der Schalie, 1973). The present analysis suggested a split between *L. bubala* and Duck River *Lithasia* occurring around four million years ago, in the middle of the Pliocene. *Lithasia bubala* appears to have coalesced as a species 274,000 years ago in the Pleistocene. The Pleistocene is often considered a period of freshwater species diversification in the east-central United States, and examples can be found in fish (Near and Keck, 2005), crayfish (Crandall and Templeton, 1999), and mussels (Watters et al., 2009).

The Buffalo River belongs to the Western Highland Rim ecoregion in the Eastern Highlands (USEPA, 2011), an area recognized as having a high diversity of flora and fauna. The Heritage Program recognizes

48 rare plant and animal species in the Buffalo River drainage, including *L. geniculata* (TDEC, 2005). While the Buffalo River itself is not seen as an area of high aquatic endemism, two endemic terrestrial beetles (*Pseudanophthalmus hesperus* Barr, 1959 and *P. occidentalis* Barr, 1959) and one endemic terrestrial annelid (*Cambarincola leptadenus* Holt, 1973) are found in the drainage (NatureServe, 2013). Additionally, one species in the freshwater mussel genus *Villosa* may also be endemic to the Buffalo River (G.T. Watters, pers. comm.). Based on NatureServe conservation status definitions, I recommend assigning *L. bubala* a G3/S3 ranking of vulnerable, given its restricted range and the ongoing plight of freshwater taxa in the United States (Johnson et al., 2013).

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LITERATURE CITED

Avise, J.C. and R.M. Ball. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. Oxford Surveys in Evolutionary Biology 7: 45–67.

Baum, D.A. and M.J. Donoghue. 1995. Choosing among alternative 'phylogenetic' species concepts. Systematic Botany 20: 563–573.

Bogan, A.E., J.M. Pierson, and P. Hartfield. 1995. Decline in the freshwater gastropod fauna in the Mobile Basin. In: E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran, and J.M. Mac (eds.) Our Living Resources: A report to the Nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington D.C., pp. 249–252.

Burch, J.B. 1982. North American freshwater snails. Identification keys, generic synonymy, supplemental notes, glossary, references, index. Walkerana 1: 217–365.

Burch, J.B. and J.L. Tottenham. 1980. North American freshwater snails. Species list, ranges, and illustrations. Walkerana 1: 81–215.

Crandall, K.A. and A.R. Templeton. 1999. The zoogeography and centers of origin of the crayfish subgenus *Procericambarus* (Decapoda: Cambaridae). Evolution 53: 123–134.

Cummings, M.P., M.C. Neel, and K.L. Shaw. 2008. A genealogical approach to quantifying lineage divergence. Evolution 62: 2411–2422.

de Queiroz, K. 2005. A unified species concept and its consequences for the future of taxonomy. Proceedings of the California Academy of Sciences 56: 196-215.

Dillon, R.T. 2011. Robust shell phenotype is a local response to stream size in the genus *Pleurocera*. Malacologia 53: 265–277.

Dillon, R.T. and J.D. Robinson. 2009. The snails the dinosaurs saw: are the pleurocerid populations of the Older Appalachians a relict of the Paleozoic Era? Journal of the North American Benthological Society 28: 1–11.

Drummond, A.J., S.Y.W. Ho, M.J. Phillips, and A. Rambaut. 2006. Relaxed phylogenetics and dating with confidence. PLoS Biology 4: e88. doi:10.1371/journal.pbio.0040088.

Drummond, A.J. and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7: 214.

Goodrich, C. 1940. The Pleuroceridae of the Ohio River drainage system. Occasional Papers of the Museum of Zoology, University of Michigan 417: 1–21.

Hijmans, R.J. 2009. DIVA-GIS 7.1.6. Software available at http://www.diva-gis.org.

Holznagel, W.E. 1998. A nondestructive method for cleaning gastropod radulae from frozen, alcohol-fixed, or dried material. American Malacological Bulletin 14: 181–183.

Jablonsky, D. 1986. Background and mass extinctions: the alteration of macroevolutionary regimes. Science 231: 129–133.

Johnson, P.J., A.E. Bogan, K.M. Brown, N.M. Burkhead, J.R. Cordeiro, J.T. Garner, P.D. Hartfield, D.A.W. Lepitzki, G.L. Mackie, E. Pip, T.A. Tarpley, J.S. Tiemann, N.V. Whelan, and E.E. Strong. 2013. Conservation status of freshwater gastropods of Canada and the United States. Fisheries 38: 247–282.

Lee, T., J.J. Kim, H.-C. Hong, J.B. Burch, and D. Ó Foighil. 2006. Crossing the Continental Divide: the Columbia drainage species *Juga hemphilli* (Henderson, 1935) is a cryptic member of the eastern North American genus *Elimia* (Cerithioidea: Pleuroceridae). Journal of Molluscan Studies 72: 314–317.

Lydeard, C., R.H. Cowie, W.F. Ponder, A.E. Bogan, P. Bouchet, S.A. Clark, K.S. Cummings, T.J. Frest, O. Gargominy, D.G. Herbert, R. Hershler, K.E. Perez, B. Roth, M. Seddon, E.E. Strong, and F.G. Thompson. 2004. The global decline of nonmarine Mollusks. BioScience 54(4): 321–330.

Lydeard, C., W.E. Holznagel, J. Garner, P. Hartfield, and M. Pierson. 1997. A molecular phylogeny of Mobile River drainage pleurocerid snails (Caenogastropoda: Cerithioidea). Molecular Phylogenetics and Evolution 7: 117–128.

Lydeard, C., and R.L. Mayden. 1995. A diverse and endangered aquatic ecosystem of the southeastern United States. Conservation Biology 9: 800–805.

Minton, R.L. and C. Lydeard. 2003. Phylogeny, taxonomy, genetics and global heritage ranks of an imperiled, freshwater snail genus *Lithasia* (Pleuroceridae). Molecular Ecology 12: 75–87.

Minton, R.L., A.P. Norwood, and D.M. Hayes. 2008. Quantifying phenotypic gradients in freshwater snails: a case study in *Lithasia*. Hydrobiologia 605: 173–182.

NatureServe. 2013. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. Available http://www.natureserve.org/explorer. (Accessed: April 14, 2013).

Near, T.J. and B.P. Keck. 2005. Dispersal, vicariance, and timing of diversification in *Nothonotus* darters. Molecular Ecology 14: 3485–3496.

Ortmann, A.E. 1924. The naiad-fauna of the Duck River in Tennessee. American Midland Naturalist 9: 18–62.

Perez, K.E. and R.L. Minton. 2008. What's in a name? Practical applications for systematics and taxonomy in freshwater gastropod conservation. Journal of the North American Benthological Society 27: 471–483.

Posada, D. 2008. jModelTest: Phylogenetic model averaging. Molecular Biology and Evolution 25: 1253–1256.

Rambaut, A. and A.J. Drummond. 2009. Tracer 1.5. Available at http://tree.bio.ed.ac.uk/software/tracer/.

Sides, J.D. 2005. The systematics of freshwater snails of the genus *Pleurocera* (Gastropoda: Pleuroceridae) from the Mobile River basin. Unpublished dissertation, University of Alabama, Tuscaloosa, 207 pp.

Stamatakis, A., P. Hoover, and J. Roguemont. 2008. A rapid bootstrap algorithm for the RAxML web-servers. Systematic Biology 75: 758–771.

Strong, E.E. and T.J. Frest. 2007. On the anatomy and systematics of *Juga* from western North America (Gastropoda: Cerithioidea: Pleuroceridae). Nautilus 121: 43–65.

Strong, E.E. and F. Köhler. 2009. Morphological and molecular analysis of '*Melania*' *jacqueti* Dautzenberg and Fischer, 1906: from anonymous orphan to critical basal offshoot of the Semisulcospiridae (Gastropoda: Cerithioidea). Zoologica Scripta 38: 483–502.

Tennessee Department of Environment and Conservation. 2005. Buffalo River watershed (06040004) of the Tennessee River Basin. Watershed water quality management plan. Six chapters plus appendices.

Tryon, G.W. 1873. Land and Freshwater Shells of North America. Part IV. Strepomatidae. Smithsonian Miscellaneous Collections 253: i–iv, 1–435.

Turgeon, D.D., J.F. Quinn, Jr., A.E. Bogan, E.V. Coan, F.G. Hochberg, W.G. Lyons, P.M. Mikkelsen, R.J. Neves, C.F.E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F.G. Thompson, M. Vecchione, and G. D. Williams. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks (2nd edition). American Fisheries Society Special Publication 26. 526 pp.

United States Environmental Protection Agency. 2011. Level III ecoregions of the continental United States (revision of Omernik, 1987). United States Environmental Protection Agency National Health and Environmental Effects Research Laboratory, Corvallis. Map M-1, various scales.

van der Schalie, H. 1973. The molluscs of the Duck River drainage in central Tennessee. Sterkiana 52: 45–55.

Watters, G.T., M.A. Hoggarth, and D.H. Stansbery. 2009. The Freshwater Mussels of Ohio. The Ohio State University Press, Columbus. 421 pp.

Wiley, E.O. and R.L. Mayden. 2000. The evolutionary species concept. In: Q. Wheeler and R. Meier (eds.) Species Concepts and Phylogenetic Theory: A Debate. Columbia University Press, New York, pp. 70–89.

APPENDIX 1

NCBI accession numbers for sequences used in this study. Minton and Lydeard (2003): AF435739 through AF435786. Sides (2005): EU106485, EU106517, EU106524, EU106525, EU106526, EU106543, EU106544, EU106545, EU106553, EU106562, EU106563, EU106564, EU106568, EU106570, EU106575. Campbell et al. (unpublished): EF587013.

Description of *Fusilaria garciai* new genus, new species (Gastropoda: Fasciolariidae: Fasciolariinae) from the western Caribbean Sea

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ABSTRACT

A new fasciolariine species is described from the western Caribbean Sea, and assigned to a new genus. Four specimens of this large species were collected from lobster traps set at 200 m depth off Roatán Island, Honduras.

Additional Keywords: Fasciolaria tephrina, Honduras

INTRODUCTION

This paper describes a new fasciolariine species collected by lobster fishermen working from Roatán Island, Honduras. Crabbed shells of the new species were collected in lobster traps set at 200 m depth off Punta Camerón, at roughly 16° N, 84° W. A new genus is proposed for this species. Specimens of *Fasciolaria tephrina* de Souza, 2002, another deepwater fasciolariine, were collected concurrently in traps set in the same area at 500 m, and color forms of this species are discussed.

MATERIALS AND METHODS

The study material was obtained from a fisherman at Roatán Island, Honduras by Dr. Emilio F. García in December, 2012. All four shells were occupied by hermit crabs and collected in lobster traps. Measurements were made with a manual vernier caliper and recorded to the nearest 0.1 mm. Examinations were carried out with a Nikon 70594 stereomicroscope. The abbreviation ANSP is used for the Academy of Natural Sciences of Drexel University of Philadelphia.

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SYSTEMATICS

Family Fasciolariidae Gray, 1853
Subfamily Fasciolariinae Gray, 1853

Fusilaria new genus

Type Species: *Fusilaria garciai* new species

Diagnosis: Shell moderately large for subfamily; protoconch large; siphonal process long. Prominent sharp columellar folds; prominent parietal ridge. Continuous and interrupted lirae present on inner side of outer lip.

Description: Adult shell moderately large for subfamily, with large protoconch and high spire. Axial sculpture of low ribs forming nodes on peripheral keel adapical to the axial midpoint of each whorl. Spiral sculpture of numerous low, fine cords. Two or three prominent columellar folds present at entrance to siphonal canal with as many as four weaker folds adapically, not always visible from outside. Siphonal canal somewhat twisted. Parietal ridge prominent with sharp edge. Inner side of outer lip with fine lirae, both continuous and interrupted (beaded).

Remarks: Snyder, Vermeij and Lyons (2012) recognized 14 genera in the subfamily Fasciolariinae. *Fusilaria* differs from all these genera; we discuss in detail those genera with Caribbean members. Three genera, all confined to the southeastern United States, contain only fossil members. *Liochlamys* Dall, 1889 and *Terebraspira* Conrad, 1862 are quite unlike *Fusilaria*, with species differing markedly in general shell morphology, but *Pliculofusus* Snyder, Vermeij and Lyons, 2012 requires comparison because that genus shares several characters with *Fusilaria*. Of the other 11 genera, only four (*Aurantilaria* Snyder, Vermeij and Lyons, 2012; *Cinctura* Hollister, 1957; *Fasciolaria* Lamarck, 1799; and *Triplofusus* Olsson and Harbison, 1953) have Recent members

occurring in the Caribbean, and of these only *Fasciolaria* has an amphi-Caribbean distribution. The other three genera barely satisfy the Caribbean criterion, *Aurantilaria* extending northward only to the southeastern corner and *Cinctura* and *Triplofusus* extending southward only to the northwestern edge of the Caribbean. One additional genus, *Granolaria*, has two living members in the eastern Pacific but has five Caribbean fossil members ranging in age from Early Pliocene to Early Pleistocene. These six genera, their Recent Caribbean members, and differences between each of those genera and *Fusilaria* are as follows:

Aurantilaria Snyder, Vermeij, and Lyons, 2012. Included species: *A. aurantiaca* (Lamarck, 1816). Principally a Brazilian species but ranges northward to the Grenadines with fossil records in Florida and the Dominican Republic. *Fusilaria* differs by having spiral cords neither prominent nor nodular, and by having a sharply edged parietal ridge.

Cinctura Hollister, 1957. Included species: *C. lilium* (Fischer von Waldheim, 1807). Principally found in the western Gulf of Mexico but occurs across the Yucatan Platform as far south as Cancun. *Fusilaria* differs by having axial sculpture on early whorls and body whorl, spiral cords on all whorls except upper part of body whorl, and some beaded lirae on inner side of outer lip. It also has a larger size.

Fasciolaria Lamarck, 1799. Included species: *F. bullisi* Lyons, 1972; *F. hollisteri* Weisbord, 1962; *F. tephrina* Souza, 2002; *F. tulipa* (Linnaeus, 1758). *Fusilaria* differs by having axial sculpture on early whorls and body whorl, discontinuous or beaded lirae on inner side of outer lip, a prominent sharply edged parietal ridge, and sharp columellar folds.

Granolaria Snyder, Vermeij, and Lyons, 2012. Two Recent species in tropical eastern Pacific but only fossil members in Caribbean region. *Fusilaria* differs by having a high spire, some beaded lirae on inner side of outer lip, and a sharply edged parietal ridge.

Pliculofusus Snyder, Vermeij and Lyons, 2012. Contains only fossil members from the late Oligocene to Pleistocene of the Atlantic sector of the southeastern United States. *Fusilaria* differs by having axial ribs that are not prominent, a relatively much longer canal, a thinner shell, spirally elongate nodes, and two or three rather than four columellar folds.

Triplofusus Olsson and Harbison, 1953. Included species: *Triplofusus giganteus* (Kiener, 1840). Principally southeastern United States and Gulf of Mexico, barely intruding in Caribbean southward to Cozumel; Neogene record of genus at Punta Gavilan, northern Venezuela (Rutsch, 1934). *Fusilaria* differs by having a very thin, lightweight shell, spiral cords that are not prominent, and some beaded lirae on inner side of outer lip.

Etymology: The name is Latinized, combining *Fusinus* and *Fasciolaria*; the gender is feminine.

Remarks: Although the columellar plicae reveal that this new genus is fasciolariine rather than fusinine, the profile of the whorls is reminiscent of the genus *Fusinus* Rafinesque, 1815, and it is this combination of features of two subfamilies that justifies creation of the new genus-level taxon. Two fusinine species that correspond in appearance to *Fusilaria* are *Fusinus galatheae* Powell, 1967 from the Kermadec Islands and *Fusinus genticus* (Iredale, 1936) from New Zealand (and possibly eastern Australia). *Fusinus galatheae* has a similar general appearance, but differs in that the canal is straight, the outer lip is angled at the periphery, and the spiral sculpture is more pronounced, spaced more widely, and proceeds up the neck. *F. genticus* also appears similar but the early axial ribs are more prominent and not suppressed on the first 4–5 teleoconch whorls.

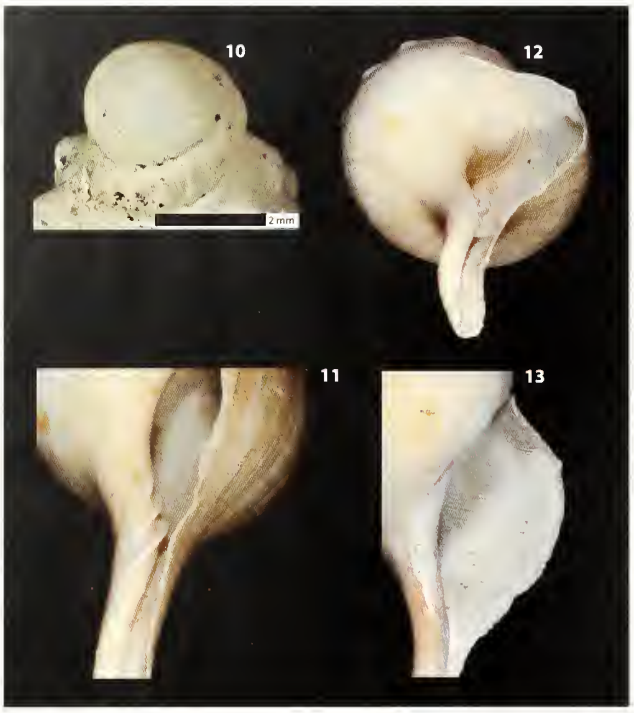
Comparison is also invited by other fasciolariine species, namely *Kilburnia scholvieni* (Strebel, 1911) from South Africa and *Australaria tenuitesta* Snyder, Vermeij and Lyons, 2012. *Kilburnia* has a larger protoconch (up to 5 mm) and short, smooth lirae on the inner side of the outer lip. The entrance fold to the siphonal canal is much more strongly expressed than the two columellar folds.

Australaria differs in several ways, but in others is quite similar. The lirae on the inner side of the outer lip are short and smooth. The most anterior fold of the siphonal canal is much more firmly expressed than the two columellar folds. In the remarks concerning the genus *Australaria* Snyder, Vermeij and Lyons (2012: 53) observed, "Although we cannot unambiguously separate the South African *Kilburnia* from the Australian *Australaria* on shell characters, we provisionally maintain them as distinct genera because of their likely long separate histories." A similar statement is probably appropriate for *Fusilaria* and *Australaria*.

***Fusilaria garciai* new species**
(Figures 1–13)

Description: Shell moderately large for subfamily, elongate, fusiform, with high spire and long siphonal process. Protoconch large, maximum diameter 3 mm, height 2.5–3.0 mm, with two bulbous cream-colored whorls, additional quarter whorl with sharp thin unornamented axial riblets, joining teleoconch smoothly. Teleoconch of 6–7 angulate whorls separated by suture, overlaid by spiral cords at the base of the whorl, with spiral keel connecting 11–12 spirally elongate, axially compressed nodules; with half whorl of wider unornamented ribs, extremely short, rounded axial ribs extending adapically from nodes on later whorls, weakening abapically; fine, very low spiral cords on all early whorls, evanescent on upper part of body whorl, with a few similar cords at end of siphonal process, oblique to process axis; about 19 cords below keel and 18 above on penultimate whorl. Outer lip thin and damaged in all

Figures 1–9. *Fusilaria garciai* new species. **1–3.** Holotype, 161.7 mm, ANSP 450735. **4–6.** Paratype, 183.0 mm, ANSP 450736. **7–9.** Paratype, 119.5 mm, García collection.



Figures 10–13. *Fusilaria garciai* new species. **10.** Protoconch, holotype, ANSP 450735. **11.** Principal columellar folds, holotype, ANSP 450735. **12.** Parietal ridge, holotype, ANSP 450735. **13.** Lirae on inner side of outer lip, paratype, ANSP 450736.

examined material; inner side of outer lip with about 60 lirae, a mix of continuous, discontinuous, and beaded, stopping short of the lip by about 3 mm; abapical lirae stronger and more coarsely beaded. Anterior-most fold to siphonal canal keel-like, with one or two additional similar folds adapical to it. In some specimens as many as four additional weak folds present, some not visible from outside. Shell color ivory with peach overtones; nodes lighter on peripheral keel with light pumpkin splotch on both sides (axially) of node, with pale orange-brown axial color stripes emanating from the nodes adapically and abapically on the body whorl. Operculum and soft parts not available for study.

Type Material: Holotype ANSP 450735, 161.7 mm, in lobster traps, depth 200 m. Paratypes: 183.0 mm, ANSP 450736; 119.5 mm (Emilio García collection), all from lobster traps at type locality.

Type Locality: Off Punta Camerón, Honduras, approximately 16° N, 84° W, depth 200 m.

Other Material Examined: 181.1 mm, same data as holotype (Emilio García collection).

Distribution: Known only from the type locality.

Etymology: The species name honors Emilio F. García of Lafayette, Louisiana. Long a student of the molluscan fauna of the Gulf of Mexico and western Caribbean, he obtained these shells, recognized them as undescribed, and was kind enough to donate the holotype and a paratype to ANSP.

DISCUSSION

Fusilaria garciai new species was collected in traps set at depths of approximately 200 m. Another large fasciolariine, *Fasciolaria tephrina*, was collected in the same area in traps set at 500 m. Although thin, the shell of *F. garciai* is strong. Repaired breaks on the last whorl suggest some sort of predation. *Fasciolaria tephrina* has a fairly wide distribution from Belize to Honduras, Nicaragua, and the northern Colombian Islands southward to San Andrés (see Miloslavich et al.: 14, table S6). It is not unreasonable to speculate that both of these species are representative of a larger widespread deep-water fauna now beginning to be explored. We expect that *Fusilaria garciai* may have a wider range in the western Caribbean than indicated by this material, and it is possible that additional material will be discovered in other parts of the Caribbean at similar depths.

Fasciolaria tephrina apparently occurs in two color forms: finely banded (Figure 14) and splotched (Figure 15). The specimen depicted in Figure 15 was collected in the same area as *Fusilaria garciai*, but in traps set at 500 m. This specimen is a heavier shell than the specimen in Figure 14, and shows signs of predation. It is remarkable that species this large are still being described from the Caribbean.

Figures 14–15. *Fasciolaria tephrina*. **14.** "Banded form," 277 mm, ANSP 450737). **15.** "Splotched form", 224.75 mm, García collection.

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LITERATURE CITED

Conrad, T.A. 1862. Descriptions of new genera, sub-genera and species of Tertiary and Recent shells. Proceedings of the Academy of Natural Sciences of Philadelphia 14(6): 284–291.

Dall, W.H. 1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80) by the U.S. Coast Survey steamer *Blake*, Lieut.- Commander C.D. Sigsbee, U.S.N. and Commander J.R. Bartlett, U.S.N., commanding. XXIX. Report on the Mollusca. Part II. Gastropoda and Scaphopoda. Bulletin of the Museum of Comparative Zoology 18: 1–492, pls. 10–40. [Reprinted 1967: Kraus Reprint Corporation, New York].

Souza, P.J.S. de. 2002. A new bathyal *Fasciolaria* (Mollusca: Caenogastropoda) from the southwestern Caribbean. Zootaxa 49: 1–7, figs. 1–12.

Fischer von Waldheim, G. 1807. Muséum-Démidoff, ou catalogue systématique et raisonné des curiositiés de la nature et de l'art, données à l'Université Impériale de Moscou par son Excellence Monsieur Paul de Démidoff. (mis en ordre systématique et décrit par G. Fischer), Tome Troisième, Végétaux et Animaux. Moscou. ix, 330 pp., 6 pls. [Classe des Mollusques, pp. 102–280].

Gray, J.E. 1853. On the division of ctenobranchous gasteropodus Mollusca into larger groups and families. Annals and Magazine of Natural History, Second Series, 11(62): 124–133, figs. 1–10.

Hollister, S.C., 1957. On the status of *Fasciolaria distans* Lamarck. The Nautilus 70: 73–83.

Iredale, T. 1936. Australian molluscan notes, No. 2. Records of the Australian Museum 19(5): 267–340, pls. 20–24.

Lamarck, [J.B.P.A.]. 1799. Prodrome d'une nouvelle classification des coquilles, comprenant une rédaction appropriée des caractères génériques, et établissement d'un grand nombre de genres nouveaux. Mémoires de la Société d'Histoire Naturelle de Paris 1: 63–91, fold out table, [as "citoyen Lamarck"].

Lamarck, [J.B.P.A]. 1816. Mollusques et polypes divers. In: Bruguière et al., 1791–1827: Tableau encyclopédique et méthodique des trois règnes de la nature. Part 23: 1–16, pls. 391–488, 431 bis, 431 bis*.

Linnaeus, C. 1758. Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteristibus, differentiis, synonymis, locis Vol. 1 Editio decima, reformata. Holmie: Laurentii Salvii. 824, iii pp.

Lyons, W.G. 1972. A new *Fasciolaria* from the northeastern Gulf of Mexico. The Nautilus 85: 96–99.

Miloslavich, P., J.M. Diaz, E. Klein, J.J. Alvarado, C. Diaz et al. 2010. Marine biodiversity in the Caribbean: regional estimates and distribution patterns. PLoS ONE 5(8): e11916. doi:10:1371/journal.pone.0011916.

Olsson, A.A. and A. Harbison. 1953. Pliocene Mollusca of southern Florida with special reference to those from north Saint Petersburg (with special chapters on Turridae by William G. Fargo and Vitrinellidae and fresh-water mollusks by Henry A. Pilsbry). The Academy of Natural Sciences of Philadelphia Monographs 8: i–v, 1–457, pls. 1–65.

Powell, A.W.B. 1967. Mollusca of the Kermadec Islands, Part 2. Records of the Auckland Institute and Museum 6: 197–200.

Rafinesque, C.S. 1815. Analyse de la nature ou tableau de l'univers et des corps organisés. Palerme. 224 pp. [In: The complete writings of Constantine Smalz Rafinesque on Recent & fossil conchology edited by W.G. Binney and G.W. Tryon. Bailliere Brothers, New York, 1864 Reprinted 1984].

Rutsch, R.F. 1934. Die Gastropoden aus dem Neogen der Punta Gavilan in Nord-Venezuela. Abhandlungen der Schweizerischen Palaeontologischen Gesselschaft 54: 1–88, pls. 1–7, part 1.

Snyder, M.A., G.J. Vermeij, and W.G. Lyons. 2012. The genera and biogeography of Fasciolariinae (Gastropoda). Basteria 76: 31–70, figs. 1–25.

Strebel, H. 1911. Zur Gattung Fasciolaria Lam. Mitteilungen aus dem Naturhistorischen Museum in Hamburg. Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 28: 1–58, pls. 1–15 (1912).

Weisbord, N.E. 1962. Late Cenozoic gastropods from northern Venezuela. Bulletins of American Paleontology 42(193): 1–672, pls. 1–48.

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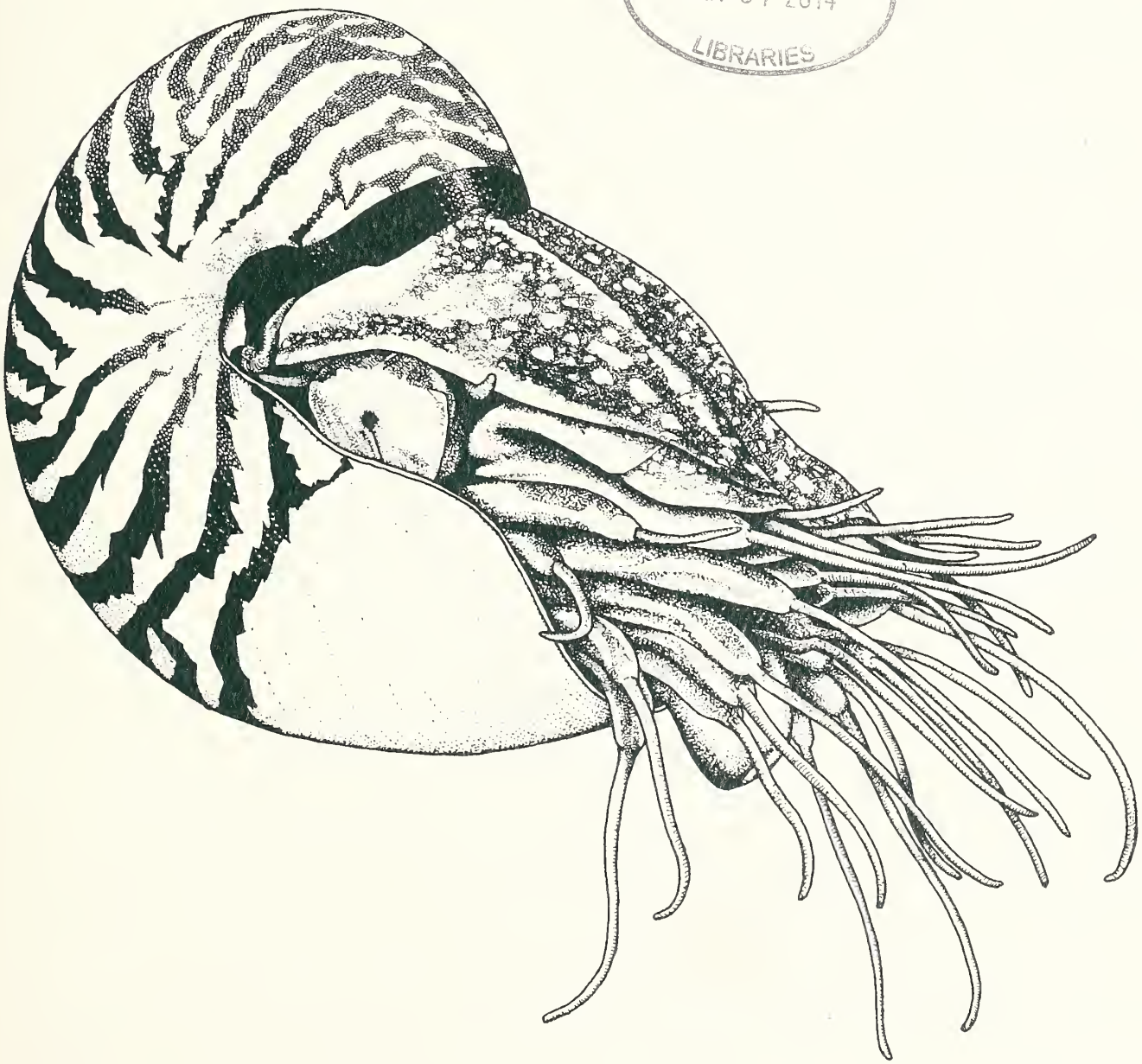

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Taxonomy and phylogeny of western Atlantic Lucinidae: new genus for *Lucina costata* d'Orbigny, 1846, a new species of *Ferrocina* and neotype designation for *Venus orbiculata* (Montagu, 1808)

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ABSTRACT

A new genus, *Clathrolucina* Taylor and Glover, is proposed for the widely distributed western Atlantic species *Lucina costata* d'Orbigny, 1846, which has previously been placed in *Codakia*, *Ctena*, and *Parvilucina*. Molecular evidence indicates a closer relationship to *Radiolucina* and *Lucinisca*. A new species, *Ferrocina garciai* Taylor and Glover, is described from submerged pinnacles off the coasts of Louisiana and Alabama. It is similar to *Ferrocina* species described from the western Pacific and, in molecular analysis clusters, with *Parvilucina* and *Bathyaustriella*. Unusual features of this species include the large ctenidia and the lateral coiled pouches of the visceral mass. A neotype is designated for *Lucina orbiculata* Montagu, 1808 aka *Ctena orbiculata*, an abundant shallow water lucinid of the western Atlantic. The original type material is missing, the type locality is erroneous and considerable doubt exists about the identity of this species.

INTRODUCTION

More than 40 species of Lucinidae, well known for their chemosymbiosis with sulphide-oxidizing bacteria housed in the ctenidia (Taylor and Glover 2006; Heide et al., 2012), are recorded from the tropical–subtropical western Atlantic, including deeper water species. Many of the shallow water species are relatively well known and have been the subject of important studies of the symbiosis (e.g. Giere, 1985; Fisher and Hand, 1984; Distel and Felbeck, 1987; Frenkiel and Mouëza, 1995; Frenkiel et al., 1996; Gros, Frenkiel and Mouëza, 1998; Gros et al., 1998, 2012; Gros Liberge and Felbeck, 2003, Brissac et al., 2009). Nevertheless, there are unresolved taxonomic and nomenclatural problems even amongst abundant lucinids of the region including their phylogenetic relationships. Greater taxonomic refinement may also be needed since molecular analyses of other bivalves such as Arcidae and Mytilidae have revealed that species previously regarded as widespread in the western Atlantic are in fact complexes of genetically distinct taxa (Lee and Ó Foighil, 2005; Marko and Moran, 2009). From morphological evidence, species complexes are suspected within Lucinidae in the *Lucina pensylvanica* group (Gibson Smith and Gibson Smith, 1982) and *Ctena orbiculata* group (Taylor et al., 2011). Additionally, offshore exploration at hydrocarbon seeps has recovered several new Lucinidae for the region (Taylor and Glover, 2009).

In this paper we have three objectives. Firstly, we clarify, using molecular evidence, the phylogenetic position of "*Parvilucina*" *costata* (d'Orbigny, 1846), an abundant species that has been variously and confusingly classified in five different genera. A new genus is proposed for this species. Secondly, we describe an unexpected new species, dredged from depths of 58–86 m off Alabama and Louisiana. This lucinid is unlike any other from the western Atlantic and is most similar to species of *Ferrocina* from the western Pacific (Glover and Taylor, 2007; in press). Thirdly, we designate a neotype for *Venus orbiculata* Montagu, 1808 (i.e. *Ctena orbiculata*) perhaps the most abundant lucinid of the subtropical-tropical western Atlantic. This is necessary because the type material is missing, the original figure is equivocal, the type locality is in eastern Scotland and there is likely a complex of morphologically similar but genetically distinct species living in the western Atlantic.

MATERIALS AND METHODS

Molecular Methods: Two new sequences from the 28S rRNA nuclear gene and mitochondrial cytB genes were obtained from a single specimen of *Ferrocina garciai* (GenBank numbers: KF793275, KF793276). Extraction of DNA, PCR methods, and sequence editing were as in Taylor et al. (2011). The new sequences were analyzed along with a subset of previously published sequences primarily from Taylor et al. (2011), although distant outgroups and multiple exemplars of species were removed. The alignment of cytB was unambiguous but 28S required alignment with MAFFT (v 6.864; Katoh et al. 2002; online: http://mafft.cbrc.jp/alignment/server/). The G-INS-I option was used with '1PAM / κ=2' because the species were from two closely related subfamilies. Gap opening penalty was 1.5 with an offset value of 0.1 as long gaps were not expected based on previous analyses. A total of 1453 bp remained in the alignment after Gblocks was used to remove ambiguously aligned regions (97% of the original 1497 positions) (0.91b, Castresana, 2000; http://molevol.cmima.csic.es/castresana/Gblocks_server.html; using options for a less stringent selection).

A species tree was constructed using concatenated sequences from both genes and Bayesian inference as implemented in MrBayes (v. 3.2.1, Huelsenbeck and Ronquist, 2001). Nucleotide substitution models for both genes were GTR+I+G as determined by MrModelTest (v 2.1, J. Nylander, http://www.abc.se/~nylander). Bayesian analyses and tests for stationarity were performed following protocols in Williams (2012).

Abbreviations: NHMUK: The Natural History Museum, London; MNHN: Muséum National d'Histoire Naturelle, Paris; PRI: Paleontological Research Institution, Ithaca, New York; USNM: National Museum of Natural History, Washington; YPM: Peabody Museum, Yale University, New Haven; H: shell height; L: shell length; PI: Protoconch 1; PII: Protoconch 2; SEM: scanning electron microscopy; T: tumidity.

RESULTS

1. New Genus for *Lucina costata*

The lucinid species often called *Ctena* or *Parvilucina costata* (d'Orbigny, 1846) is widely distributed in the western Atlantic, ranging from Bermuda, North Carolina, through the Caribbean and Central America to Rio de Janeiro (Britton 1970; Schweimanns and Felbeck, 1985; Rios, 1994; Vokes and Vokes, 1984; Redfern, 2001; Hauser et al., 2007; Mikkelsen and Bieler, 2007). It is often abundant in shallow-water seagrass beds (Jackson, 1972; 1973). Despite being a common and widely distributed species, its systematic position is uncertain. It has been variously placed in the genera *Codakia*, *Ctena*, *Jagonia*, *Parvilucina*, and *Lucina* in taxonomic and biological literature. In the last major taxonomic revision of western Atlantic species, Bretsky (1976) listed some shell characters to differentiate *L. costata* from *Ctena* but placed it questionably in *Parvilucina*.

In common with all other investigated Lucinidae, *Lucina costata* possesses symbiotic sulphide-oxidizing bacteria housed in the ctenidia. Details of ctenidial structure and location of symbionts in the species were given by Giere (1985) and the bacteria characterized molecularly by Distel et al. (1994) (as *Codakia costata* GenBank L25712). Several other anatomical features of the species were described by Allen (1958).

Samples of *L. costata* from Guadeloupe and Bocas del Toro, Panama, were included in a molecular analysis of a wide range of lucinid species with broad taxonomic coverage (Taylor et al., 2011). The results (Figure 1) indicate that it does not group with *Codakia*, *Ctena*, *Lucina*, or *Parvilucina* but instead forms a clade with *Radiolucina* and *Lucinisca* species within the subfamily Lucininae. We are therefore introducing a new genus to accommodate *Lucina costata* and two fossil species.

SYSTEMATICS

Family Lucinidae Fleming, 1828
Subfamily Lucininae Fleming, 1828

Clathrolucina new genus Taylor and Glover

Type Species: *Lucina costata* d'Orbigny, 1846 here designated.

Diagnosis: Shell small, L to 15 mm, subcircular, inflated. Sculpture of numerous radial ribs of varying thickness, prominent ribs often bifurcated, crossed by fine commarginal lamellae. Lunule heart shaped, short. Hinge with two cardinal teeth and large anterior and posterior lateral teeth in each valve. Anterior adductor scar broad, medium long, ventrally detached from pallial line for about ½ length. Inner shell margin finely dentate.

Etymology: *clathrus*, Latin for basket and *Lucina*, in reference to the basket weave appearance of the external sculpture.

Remarks: Molecular analysis (Figure 1) shows that *Clathrolucina costata* falls within the subfamily Lucininae and forms a subclade with *Radiolucina* and *Lucinisca* (Taylor et al., 2011) rather than its previous placements within *Ctena* and *Codakia* based on morphology. There are superficial shell characters in common with *Ctena* Mörch, 1861 (type species: *Codakia (Jagonia) mexicana* Dall, 1901) including the bifurcating radial ribs and posterior dorsal areas that lack radial sculpture. The anterior adductor scar of *Ctena* is longer and more widely detached from the pallial line (Figure 25). *Jagonia* Récluz, 1869 (type species: *Venus eburnea* Gmelin, 1791) has been used for *C. costata* by earlier authors such as Dall (1901) and Chavan (1937) but it is now considered a junior synonym of *Ctena* (Bretsky, 1976). In more recent publications, *Clathrolucina costata* has been classified

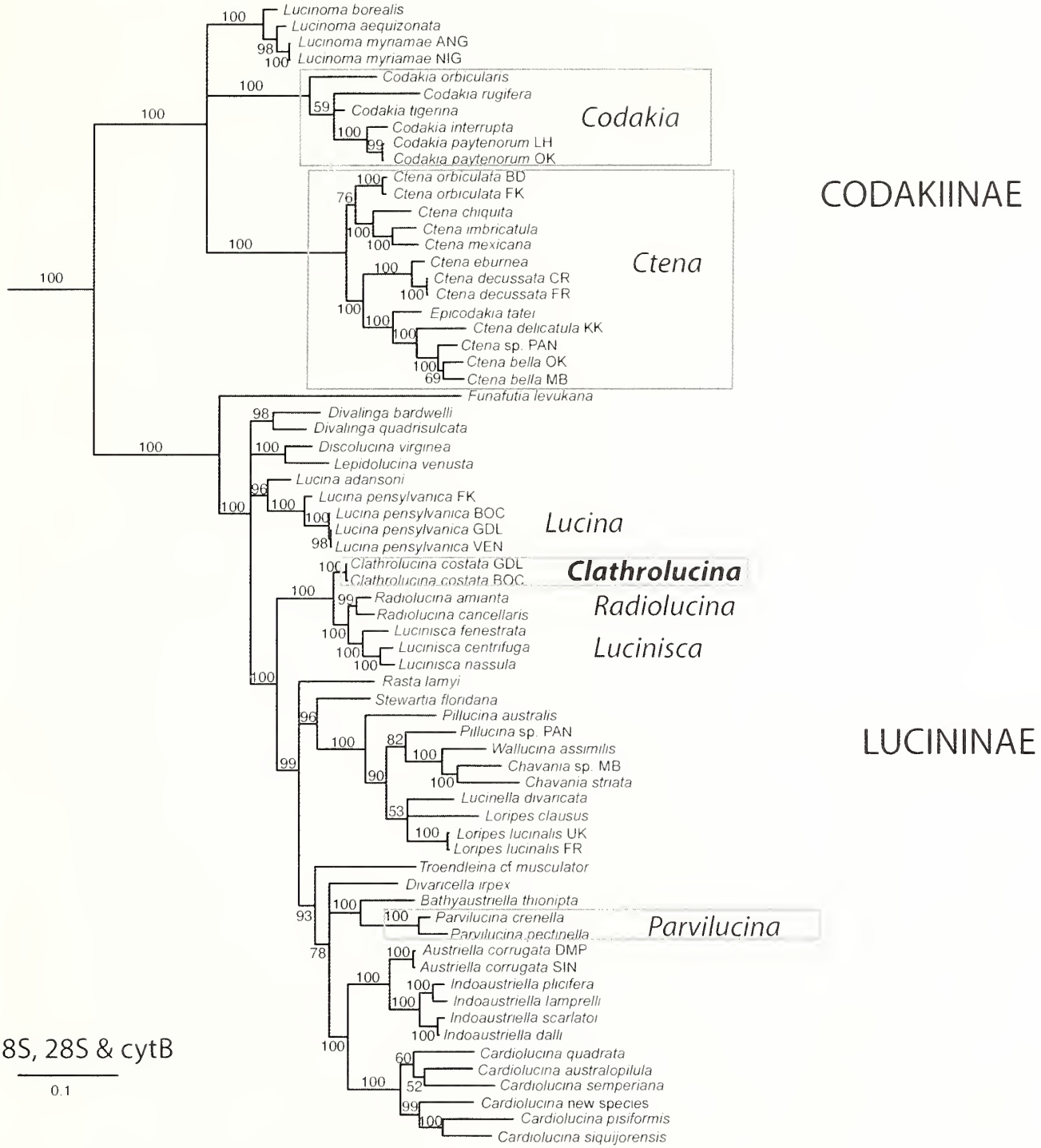


Figure 1. Molecular phylogeny of Lucinidae produced by Bayesian analysis of concatenated sequences of 18S rRNA, 28S rRNA, and cytochrome *b* genes (adapted from inset in figure 4 from Taylor et al., 2011). The position of *Clathrolucina costata* is highlighted, as are the genera where it has previously been assigned. Subfamily names are indicated on the right. Further details given by Taylor et al. (2011).

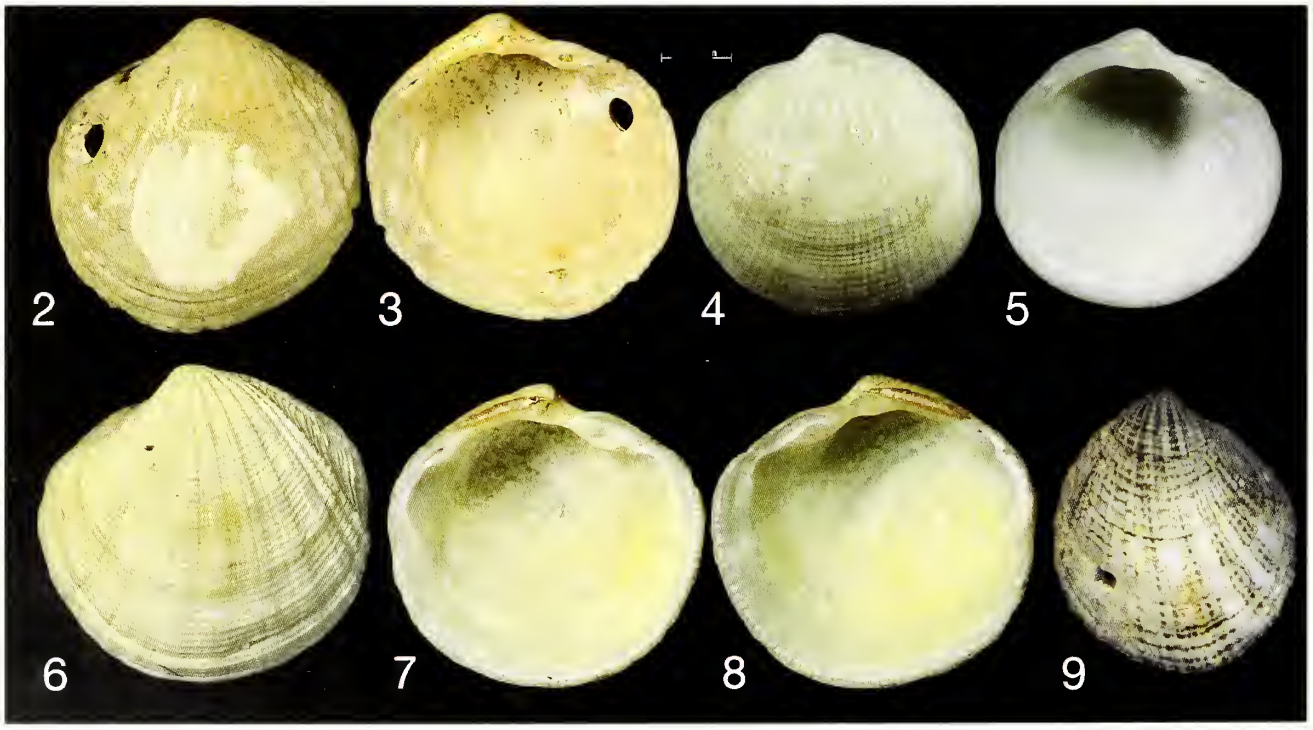
as a species of *Parvilucina* Dall, 1901 (type species: *Lucina tenuisculpta* Carpenter, 1864, from the northeastern Pacific). However, in the molecular analysis, although *C. costata* and two western Atlantic *Parvilucina* species occur in the same major lucinid clade (subfamily Lucininae; Taylor et al., 2011), they are not closely related. *Parvilucina* species have fine radial ribs that do not bifurcate, an extremely short anterior adductor

scar detached for only about ¼ of length (Figure 26), and the shell margin is finely denticulate. *Clathrolucina* groups with *Lucinisca* Dall, 1901 (type species: *Lucina nassula* Conrad, 1846) and *Radiolucina* Britton, 1972 (type species: *Phacoides (Bellucina) amiantus* Dall, 1901) from the western Atlantic. *Lucinisca* has fine, non-birfurcating radial ribs, crossed by low, thin commarginal lamellae forming raised scales where they cross the radial ribs. Radial ribs project beyond the ventral shell margin as denticles. The lunule in the type species is short and deeply inset and the anterior adductor scar is ventrally detached for about ½ of its length (Figure 24). The three living species of *Radiolucina* were recently reviewed by Garfinkle (2012); *Radiolucina amianta* has about 9–11 prominent radial ribs with deep interspaces, a short heart-shaped lunule with the anterior adductor scar detached for about ½ of length (Figure 23). The inner shell margin is coarsely denticulate. Dall (1901) originally placed *R. amianta* in a subgenus *Bellucina* (= *Cardiolucina* Sacco, 1901) but Britton's (1972) recognition of *Radiolucina* is corroborated by molecular results in which *Radiolucina amianta* and *R. cancellaris* are distantly separated from *Cardiolucina* species (Taylor et al., 2011).

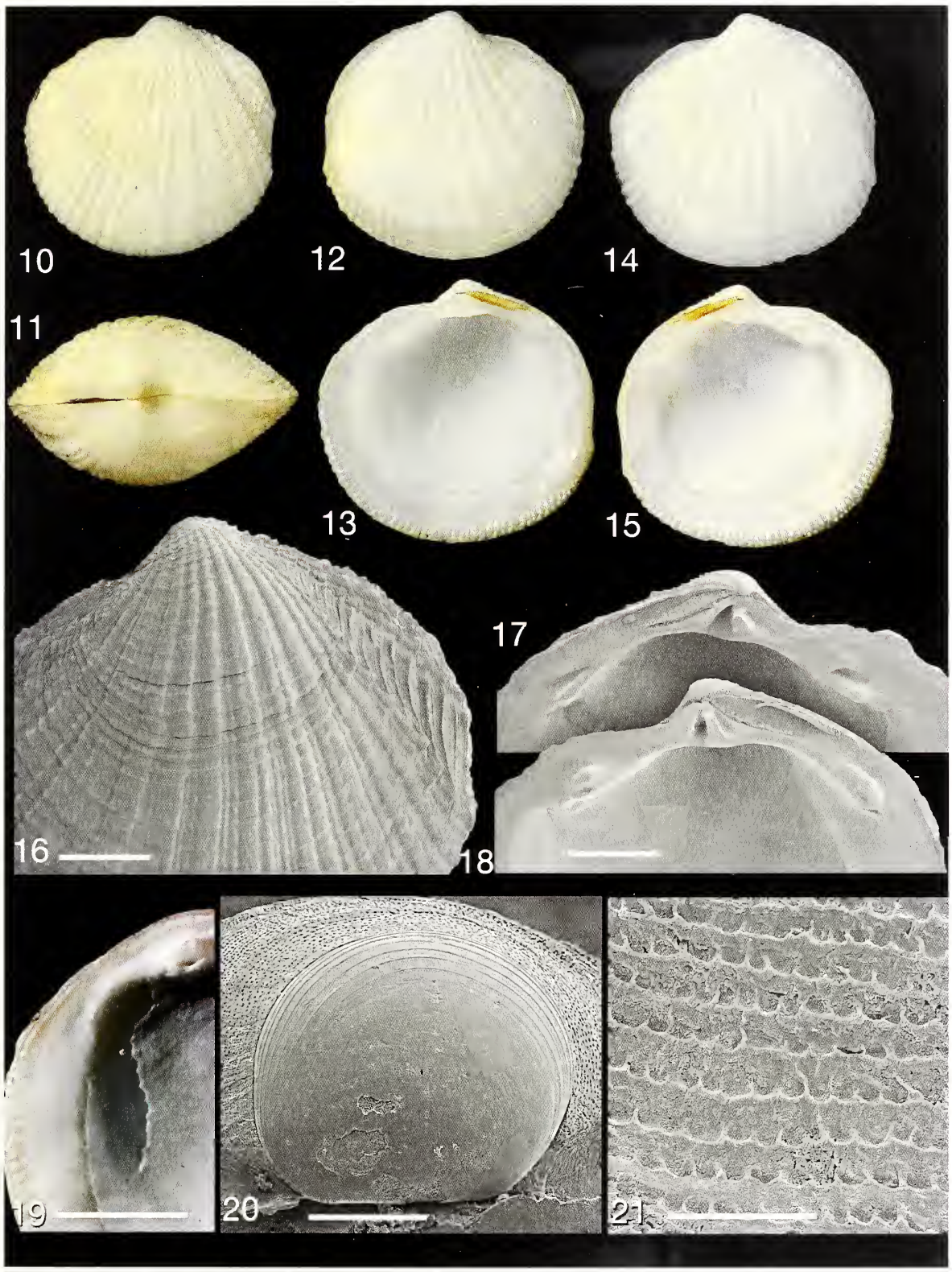
Included Species: *Codakia (Jagonia) vendryesi* Dall, 1903 from the Pliocene, Bowden Formation, Jamaica (3 syntypes USNM 135720; see Woodring 1925: 109 pl. 14, figs. 1–4.) and *Codakia (Jagonia) umbonicostata* Weisbord (1964: 234, pl. 31, figs 7–8) from the Pliocene of Venezuela (holotype PRI 1519a).

***Clathrolucina costata* (d'Orbigny, 1846)**
(Figures 2–22)

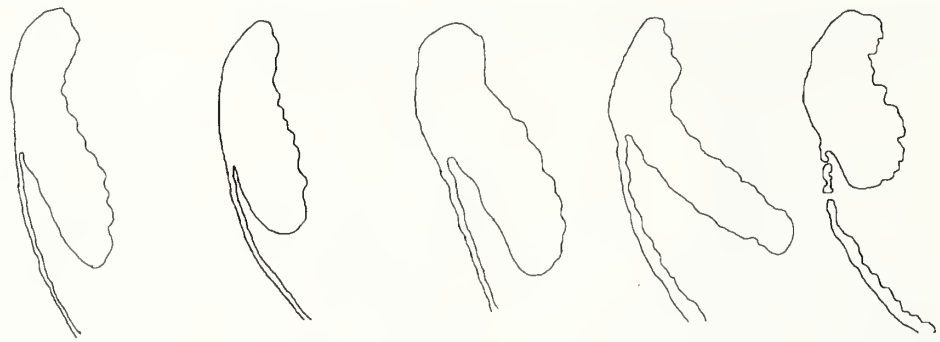
Lucina costata d'Orbigny, 1846: 586, 1853: 296, pl. 27, figs 40–42.
Lucina antillarum Reeve, 1850: pl. 10, fig. 37.
Lucina textilis Philippi, 1850: 104, pl. 2, fig. 7.
Lucina nux Verrill and Bush, 1900: 518, pl. 58, figs 12, 13.
Codakia (Jagonia) costata.—Dall, 1901: 800; Lamy, 1920: 262–263).
Jagonia (Jagonia) costata.—Chavan, 1937: 260.
Codakia (Codakia) costata.—Abbott, 1954: 390; Vokes and Vokes, 1984: 38, pl. 38, fig. 5.
Codakia costata.—Allen, 1958: 426, fig. 64; Warmke and Abbott, 1961:178; Abbott, 1974: 460, fig. 5298; Rios, 1994: 253, pl. 87, fig. 1236.
Parvilucina (Parvilucina) costata.—Britton, 1972: fig. 5.
Lucina (Parvilucina?) costata.—Bretsky, 1976: 263, pl. 28, figs 1–5.
Parvilucina costata.—Redfern, 2001: pl. 91, figs. 887 A, B; Jensen and Pearce, 2009: 330; Turgeon et al., 2009: 727.
"Parvilucina" costata.—Mikkelsen and Bieler, 2007: 234.
Ctena orbiculata.—Tunnell et al., 2010: 341 and figure, non Montagu, 1808.



Figures 2–9. Type material of *Clathrolucina costata*. **2–3.** Exterior and interior of the holotype of *Lucina costata*, Rio de Janeiro, Brazil, NHMUK 1854.12.4.765, L= 12.8 mm. **4–5.** Paratype of *L. costata*, exterior and interior of left valve, St. Thomas, NHMUK 1854.10.4.564. L = 8.9 mm. **6–8.** Syntype of *Lucina antillarum* NHMUK1963192-3, exterior of left valve and interior of left and right valves L = 12.0 mm. **9.** Holotype *Lucina nux* Bermuda, YPM 8760, exterior of right valve. L = 7 mm.



Figures 10–21. *Clathrolucina costata* from Bocas del Toro, Panama, NHMUK 20130562. **10.** Exterior of left valve, L = 8.1 mm. **11.** Dorsal view of shell in Figure 10. **12–13.** Exterior and interior of right valve, L = 8.3 mm. **14–15.** Exterior and interior of left valve, L = 8.3 mm. **16.** Detail of sculpture. Scale bar = 1.0 mm. **17–18.** Detail of hinge teeth of left and right valves. Scale bar = 1.0 mm. **19.** Detail of anterior adductor muscle scar. Scale bar = 2 mm. **20.** Protoconch, note micropunctae of post-settlement shell. Scale bar = 50 μm. **21.** Microsculpture. Scale bar = 10 μm.



Figures 22–26. Outline drawings of anterior adductor muscle scars. Traced from digital images.

Types: *Lucina costata*, holotype, NHMUK1854.12.4.765, one left valve, L = 12.8 mm, H = 12.7 mm, T = 4.5 (Figures 2–3); paratypes NHMUK 1854.10.4.564, St Thomas, US Virgin Islands, 8 valves (4R, 4L); Gray Cat No. 497 (Figures 4–5); *Lucina antillarum*, 3 whole syntypes, NHMUK 1963192-3 (Figures 6–8), L = 12.0 mm, 15.1 mm, 12.4 mm, St. Johns, Antigua; *Lucina nux* holotype, YPM 8760, single right valve, L = 7 mm, H = 8 mm, T = 3 mm (Figure 9).

Type Locality: d'Orbigny (1846: 586) cited Baie de Rio Janeiro near St Christophe and gave other localities – Antilles and Cuba.

Description: Shell small (L to 15.2, H to 14.3 mm), subcircular (H/L=0.95, n=10) moderately inflated, posterior margin slightly truncated, umbones prominent. Sculpture of numerous (ca. 35) rounded radial ribs, varying in width, that occur in bundles of two to three ribs, sometimes bifurcated ventral to umbo (Figure 16). Ribs crossed by low, regularly spaced commarginal lamellae. Posterior dorsal area without radial ribs but with more prominent commarginal lamellae, posterior dorsal margin with two low radial ribs with raised scales. Anterior dorsal area marked by lower and broader radial ribs. Lunule short, heart shaped, smooth, slightly asymmetrical with right side larger. Ligament, external, short, set in shallow groove. Microsculpture of rows of shallow pits (Figure 21) or micropunctate in juvenile shell (Figure 20). Protoconch (Figure 20): PI = 121 μm, PI + PII = 146 μm, PII with 5–8 growth increments. Hinge (Figures 17–18): LV with 2 cardinal teeth, the anterior larger, prominent anterior and posterior lateral teeth; RV with 2 cardinal teeth, the posterior much larger and slightly bifid, anterior and posterior laterals prominent. Anterior adductor muscle scar broad (Figures 19, 22), medium-long, with rounded ventral tip, ventrally detached from pallial line for about ½ of length and diverging at an angle of 5–10°. Posterior adductor scar reniform. Pallial blood vessel track visible. Pallial line entire. Inner shell margin finely denticulate. Colour yellowish-white externally, white internally.

Distribution: Western Atlantic and throughout Caribbean from North Carolina to Santa Catarina, Brazil (Britton, 1970; Rios, 1994).

Remarks: The holotype is a worn shell in poor condition but has the features of the species. Other d'Orbigny specimens in NHMUK from St. Thomas and regarded as paratypes are worn but in better condition. No locality was given for *Lucina textilis* Philippi, 1850 and the type has not been located. Syntypes of *Lucina antillarum* Reeve, 1850 are in good condition and one is figured (Figures 6–8). *Lucina nux* Verrill and Bush, 1900 described from Bermuda (Figure 9) is regarded as a higher than long shape variant of *C. costata*.

2. A New Species from the Northern Gulf of Mexico

This unusual species, a surprising addition to the shallow water bivalve fauna of the Gulf of Mexico sent to us by Emilio Garcia, was dredged from submarine pinnacles on the Alabama and Louisiana shelf.

SYSTEMATICS

Subfamily Lucininae Fleming, 1828

Ferrocina Glover and Taylor, 2007

Type species: *Ferrocina multiradiata* Glover and Taylor, 2007.

Diagnosis: Shell to 20 mm, thin, subovate, posteriorly truncate, sculpture of numerous fine to indistinct radial ribs crossed by fine commarginal threads. Hinge plate thin, small single cardinal tooth in RV, two in LV, lateral teeth small or absent. Anterior adductor scar short, detached for 1/3 of length. Interior shell margin coarsely to finely dentate. Color bright to pale orange or rusty

red-brown, external color paler, often blotchy, stronger in umbonal area.

Included species: *Ferrocina multiradiata*, (Vanuatu, Fiji, New Caledonia): *Ferrocina* new species Glover and Taylor (in press), Philippines; and *F. brunei* from off Brunei (Taylor and Glover, 2013).

Remarks: This distinctive, rare, and highly colored genus with fine radial ribs was originally described from Fiji, New Caledonia, and Vanuatu with other species known from the Philippines and Brunei.

***Ferrocina garciai* Taylor and Glover new species**
(Figures 27–44)

Type Material: Holotype (Figures 27–34), USNM 1227857, L = 19.7 mm, H = 19.0 mm, T = 5.2 mm, from type locality; Paratype 1 (Figures 35–37), USNM 1227858, L = 13.9 mm, H = 11.7 mm, T = 3.5, off Alabama, 29°15.681″ N, 88° 20.237″ W, 78–86 m, dredged by R/V Pelican, 27 August 2012; Paratype 2 (Figures 38–39), Emilio García collection 30783, L = 11.7 mm, from type locality.

Type Locality: USA, northern Gulf of Mexico, off Louisiana, 27°56.835′ N, 92°01.464′ W, 58 m, rubble, dredged by R/V Pelican, 26 August 2012.

Description: Small, L = 14.0 mm, H = 11.7 mm, subcircular, slightly longer than high, less mature paratypes more elongate with posterior margin truncate; thin-shelled, moderately inflated, T/L = 0.26. Shallow posterior sinus and posterior dorsal area. Sculpture of numerous fine, low, radial ribs that become obscure on ventral parts of shell, commarginal sculpture of growth lines and halts. Posterior dorsal area without radials. Protoconch (Figure 32): PI =113 μm, PI+PII =160 μm, PII with many growth increments. Lunule long, slightly asymmetric, larger in RV. Ligament long, set in shallow groove. Hinge narrow: RV with single cardinal tooth and irregular anterior folds; tiny posterior lateral teeth present on smaller paratype; LV with two cardinal teeth and anterior folds but posterior laterals present on paratype. Anterior adductor scar medium long, ventrally detached from pallial line for ½ of length at angle of ca. 10° (Figure 40). Pallial line entire, dorsally lobate. Posterior adductor scar ovoid. Impression of pallial blood vessel prominent, broad, terminating ventral to anterior adductor scar (Figures 40–41). Shell margin finely dentate and linearly grooved. Exterior color pale pink-orange to off white, umbonal area darker. Interior colour uniformly bright apricot-orange, extreme shell margin creamy white.

Anatomy: Very large, thick ctenidal demibranchs occupying most of mantle cavity (Figure 42). Mantle gills absent. Foot large, fat, with short heel. Body wall immediately anterior to the foot extended on each side into posteriorly directed "ramshorn-like" coiled projection (Figures 43–44). Labial palps as short ridges. Rectum passing dorsally and posterior to posterior adductor muscle. Posterior exhalant aperture with an inverted tube, inhalant aperture edged with papillae on middle mantle fold. Posterior mantle fusion short.

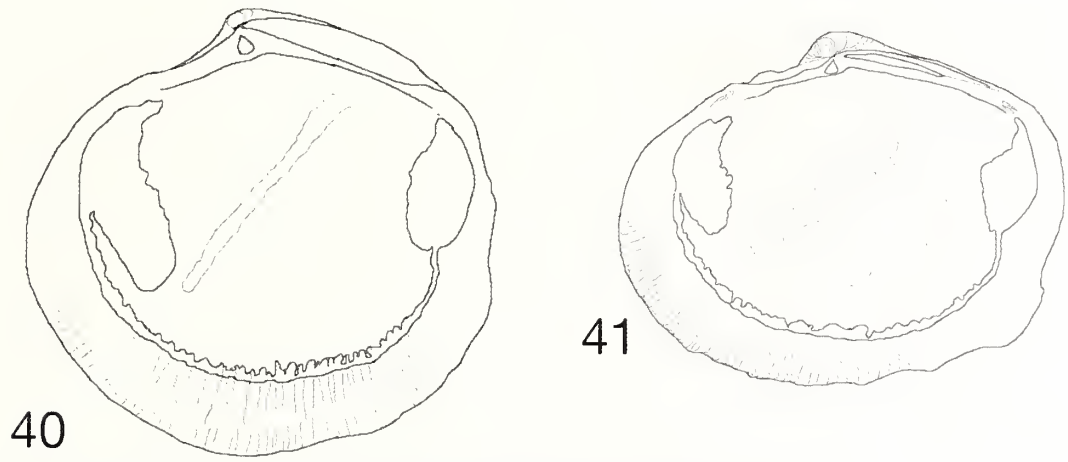
Phylogenetic Position: The results of a molecular analysis using sequences from two genes, 28S rRNA and cytochrome B (Figure 45), show the position of *Ferrocina garciai* (tissue from holotype) in relation to a diverse range of lucinid species from the subfamilies Codakiinae and Lucininae. Other more distantly related lucinid subfamilies of Pegophyseminae, Leucosphaerinae, and Myrteinae (see Taylor et al., 2011) were excluded from this analysis. The results show that *Ferrocina garciai* belongs in the Lucininae and that it is sister to two species of *Parvilucina* from the western Atlantic (PP=100%). This subclade is sister to *Bretskya* sp. and *Bathyaustriella thionipta* (PP=100%). The four genera are in turn a sister clade to *Troendleina* and *Epicodakia falklandica* although support is lower (PP=82%).

Bretskya (type species: *B. scapula* Glover and Taylor, 2007) is an Indo-Pacific genus of irregularly shaped lucinids that are strongly associated with sunken wood (Glover and Taylor, 2007; in press). *Bathyaustriella thionipta* is recorded from a 500 m deep hydrothermal vent on the Kermadec Ridge off New Zealand (Glover et al., 2004). *Troendleina* (type species: *T. marquesana* Cosel and Bouchet, 2008) includes several deeper water species (150–800 m) from the Pacific Ocean (Cosel and Bouchet, 2008, Glover and Taylor, in press). *"Epicodakia" falklandica* Dell, 1964 from the southern Atlantic occurs at depths of 100–400 m but the molecular results show that it should not be classified in the Codakiinae as *Epicodakia* but in the Lucininae with uncertain generic placement. The two *Parvilucina* species analyzed are known from shallow water habitats (1–100 m) in the western Atlantic.

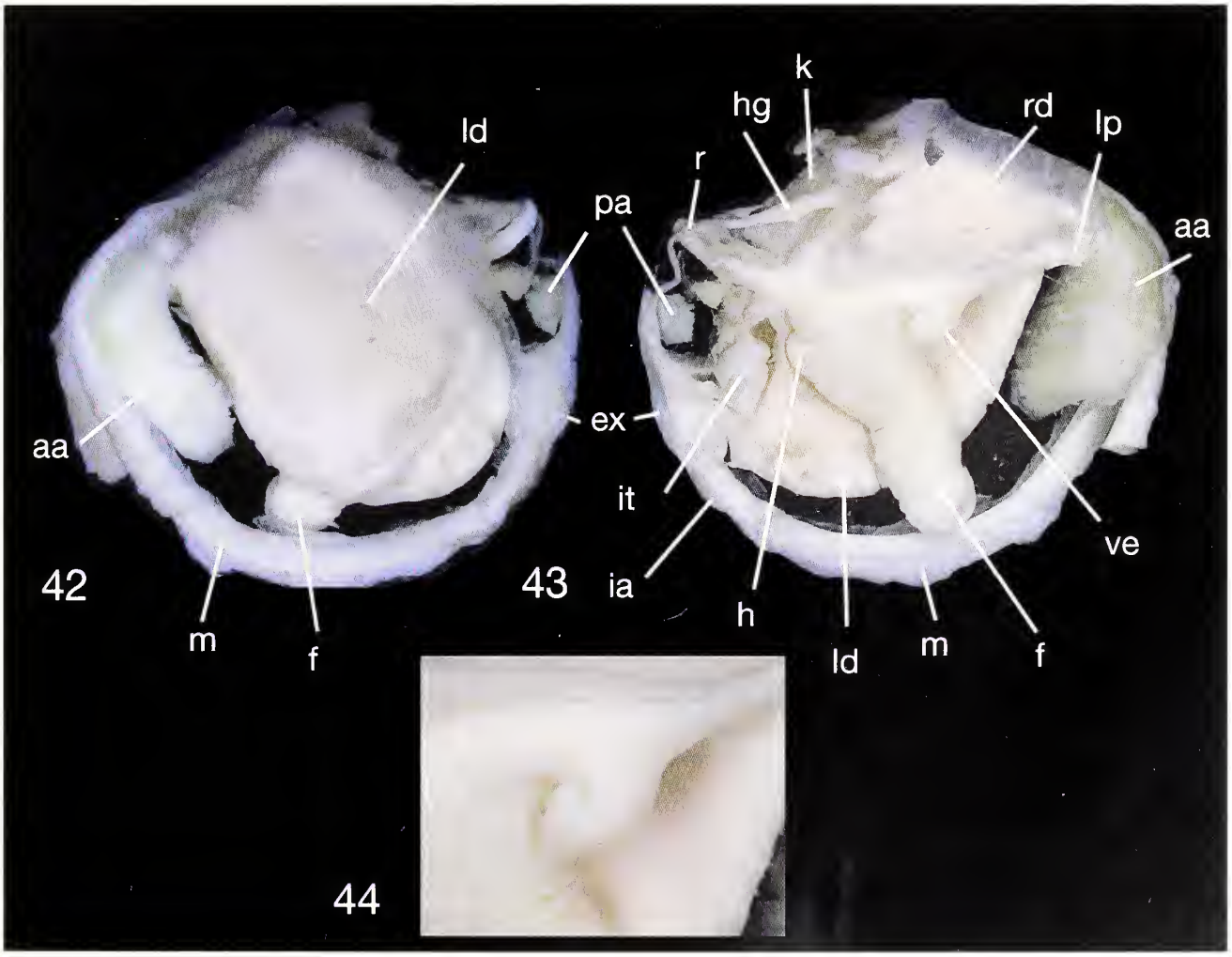
Distribution and Habitat: The three individuals of *Ferrocina garciai* were dredged from submerged calcareous pinnacles and banks at depths of 58–86 m off Louisiana and Alabama. These pinnacles occur along the northern Gulf of Mexico shelf from Alabama to Texas and form islands of hard substrate surrounded by mud (Parker and Curray, 1956). The unusual molluscan faunas of the pinnacles, including many endemic species and new records for the Gulf, have been documented by Garcia (2000; 2008) and Garcia and Lee (2002; 2013).

Remarks: Although presently known from only three specimens, *Ferrocina garciai* is a highly distinctive species and cannot be confused with any other lucinid from the western Atlantic. It differs from the type species *Ferrocina multiradiata* (Vanuatu, Fiji, New Caledonia) (Figures 46–47), depth range 80–400 m, in having finer, less prominent radial ribs and differs in shape and ribbing from a new *Ferrocina* species from the Philippines (Glover and Taylor, in press). The

Figures 27–39. *Ferrocina garciai*. **27–28.** Exterior of right and left valves of holotype, L = 19.7 mm. **29.** Dorsal view of holotype. **30–31.** Interior of right and left valves of holotype. **32.** Protoconch of holotype, boundary between P1 and P11 indicated with arrow. Scale bar = 50 µm. **33–34.** Details of hinge of left and right valves of holotype (SEM). Scale bar = 2 mm. **35.** Exterior of left valve of paratype 1. L = 13.9 mm. **36–37.** Interior of left and right valves of paratype 1. **38–39**. Exterior and interior of left valve of paratype 2, L = 11.7 mm.



Figures 40–41. Outline drawings of shell interiors of *Ferrocina*. **40.** Holotype. **41.** Paratype 1.



Figures 42–44. *Ferrocina garciai*, body of holotype. **42.** Left side with mantle removed showing large, thick, left ctenidial demibranch. **43.** Right side with mantle and part of right demibranch removed showing foot and coiled lateral visceral extension. **44.** Detail of ramshorn visceral extension. Abbreviations: **aa,** anterior adductor muscle; **ex,** exhalant aperture; **f,** foot; **h,** heel of foot; **hg,** hindgut; **ia,** inhalant aperture; **it**, invertible tube of posterior exhalant aperture; **k,** kidney; **ld,** left demibranch; **lp,** labial palps; **m,** mantle margin; **pa,** posterior adductor muscle; **r,** rectum; **rd,** right demibranch; **ve,** visceral 'ramshorn' extension.

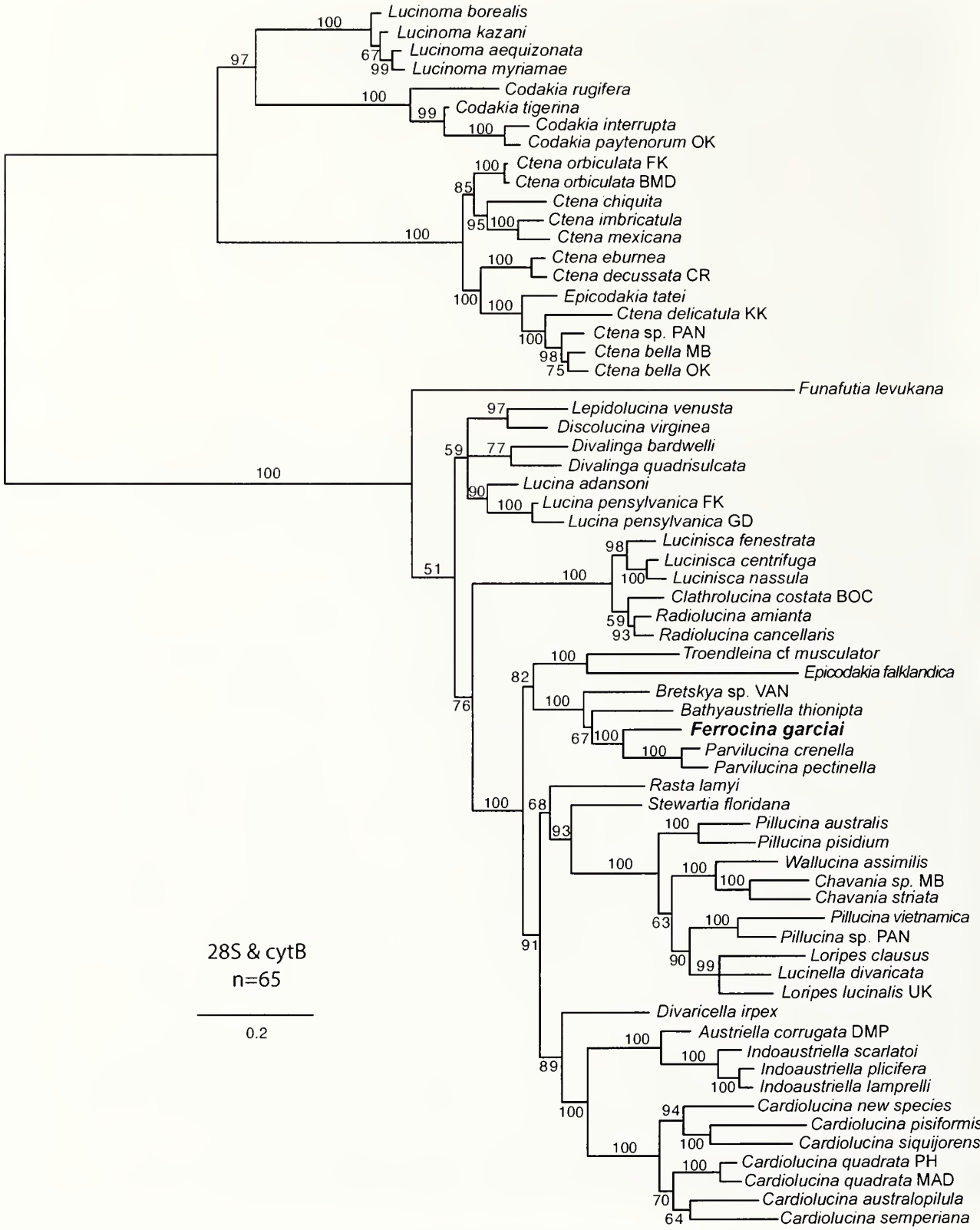
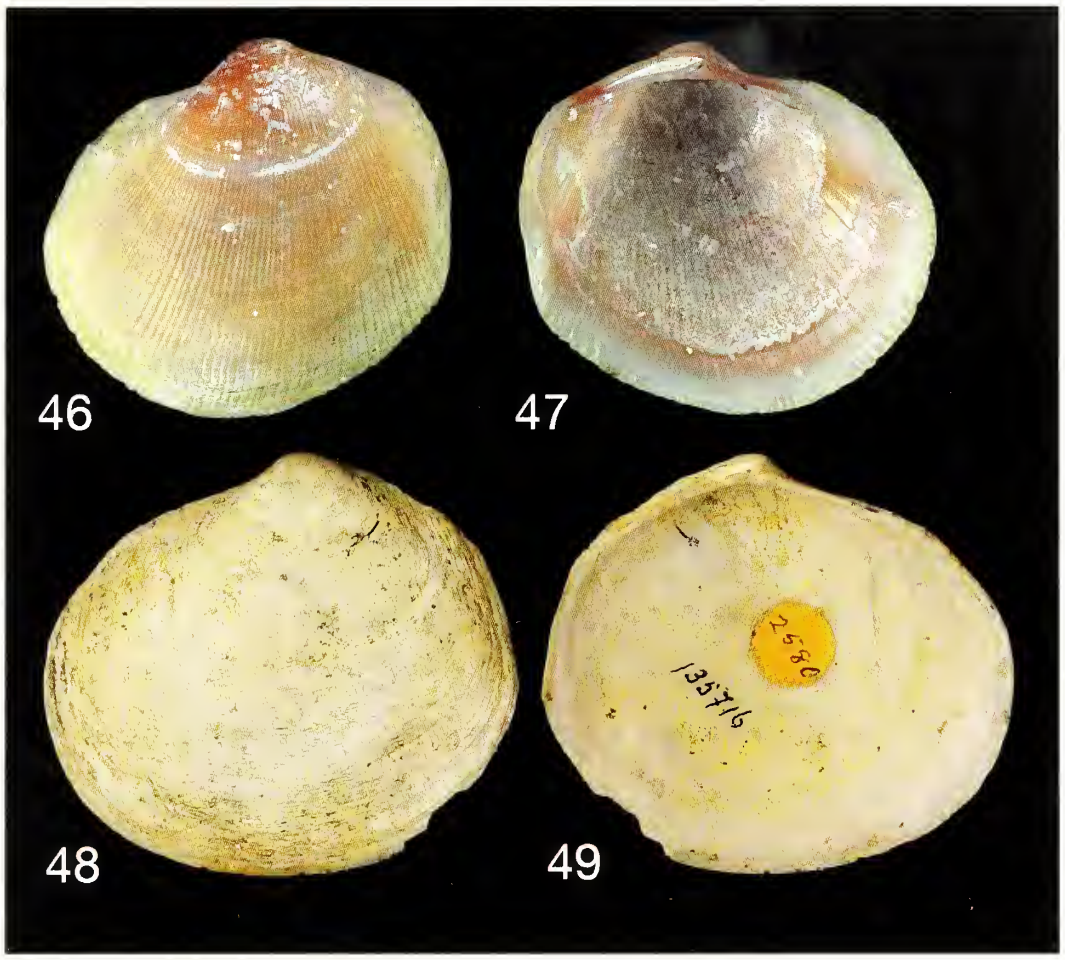


Figure 45. Molecular phylogeny of Lucinidae produced by Bayesian analysis of concatenated sequences of 28S rRNA, and cytochrome *b* genes including new sequences for *Ferrocina garciai*. Only lucinids from subfamilies Codakiinae and Lucininae included in the analysis. Locality and GenBank details of other lucinid taxa given in Taylor et al. (2011). GenBank numbers for *Ferrocina garciai*: 28S rRNA KF793276, cytochrome b KF793275.



Figures 46–49. Other species discussed under the "Remarks" for *Ferrolucina garciai*. **46–47.** *Ferrocina multiradiata* Glover and Taylor, 2007, holotype Vanuatu, 90–200 m, MNHN, exterior and interior of left valve, L = 11.2 mm. **48–49.** Syntype of *Codakia (Jagonia) pertenera* Dall, 1903, exterior and interior of left valve, L = 35 mm, USNM 135716, Pliocene, Bowden Formation, Jamaica.

juvenile paratype shells of *F. garciai* have stronger radial ribs and a shape more similar to *F. multiradiata*.

The curled body extension of *F. garciai* is similar to that described from *Bathyastriella thionipta*, a species from a hydrothermal vent on the Kermadec Ridge, New Zealand (Glover et al., 2004). *Bathyanstriella thionipta* also has very large enveloping ctenidial demibranchs and a papillate inhalant aperture. We have no anatomical data for the type species *Ferrocina multiradiata* but the recently described, small, *Ferrocina brunei* from off Brunei, Borneo (Taylor and Glover, 2013) also has the curled body extension but the demibranchs are relatively small. *Troendleina* cf. *musculator* from the Philippines has the visceral mass extended into a ventral lobe and *Parvilucina crenella* has prominent lateral pouches to the visceral mass (unpublished observations) that may be homologous with the curled body extensions of *Ferrocina*. Visceral extensions may be an apomorphy of this subclade of Lucininae.

Ferrocina garciai has many shell features similar to the *Ferrocina* species known from the tropical Pacific, but it is a surprising addition to the western Atlantic fauna because the western Pacific species are also rare and known from only a few specimens. However, there is a probable fossil antecedent in the Caribbean (Figures 48–49). This is *Codakia (Jagonia) pertenera* (Dall, 1903: 1347 pl. 51, fig. 4., four syntypes, USNM 135716) from the Late Pliocene, Bowden Formation of Jamaica, later reclassified as *Myrtaea (Myrteopsis) pertenera* by Woodring (1925: 113, pl. 14, figs 13–16). Subsequently, Bretsky (1976: 284) discussed the species, apparently not recorded from mainland North America and supported an assignment to *Ctena*. It is larger than *F. garciai* (L = 35 mm) and the life color is unknown but it is similar in shape, dentition, and anterior adductor scar, with weak radial ribs on the dorsal part of the shell, and (according to Woodring) the inner shell margin is sometimes slightly fluted.

Etymology: Named for Emilio García who collected this distinctive species.

3. Neotype for *Venus orbiculata* Montagu, 1808 (= *Ctena orbiculata*)

Ctena orbiculata (Montagu, 1808) is one of the most abundant shallow water bivalves of the western Atlantic (Britton, 1970; Bretsky, 1976; Jackson, 1972, 1973) with a reported geographical range from Bermuda to Brazil. *Venus orbiculata* was described by Montagu (1808: 42) from a locality on the east coast of Scotland: "Found on the shore near Dunbar by Mr Laskey." No *Ctena* species are known to live around Scotland or the British Isles and the record is regarded as adventitious despite findings of two shells of the Mediterranean *Ctena decussata* (da Costa) from the Scilly Islands and Cornwall – see McMillan, 1971. How the species came to be recorded from Dunbar is a mystery. Dunbar is on the eastern coast of Scotland, to the east of Edinburgh and in the late 18th and 19th centuries was a busy fishing port and for a while, a whaling port. Western Atlantic mollusc species occasionally wash up on British shores but they usually occur on the west coast (Oliver et al., 2009). The specimen could have been dumped from ship ballast or there was an accidental confusion of localities. Cleevely (1995: 391) noted that collectors such as Laskey from whom Montagu obtained shells are known to have been less than scrupulous over the provenance of their specimens.

Original Description from Montagu (1808 p. 42): *"Shell white, orbicular, depressed, and cancellated: the umbo remarkably small, beneath which is a minute cordiform depression. Inside white; margin plain, teeth, two primary approximate, and one remote standing transverse; the margin where the lateral tooth is placed projects into an angle. Diameter five eighths of an inch* (approx. 16 mm). *The shell has probably been confounded with* Venus tigerina, *but it differs somewhat in contour, is not so flat, more orbicular, and more coarsely decussated, and the lateral tooth is more remote than in* tigerina. *Found on the shore near Dunbar, by Mr Laskey."*

Since Dall (1901) the name has been accepted for the western Atlantic species and the type locality of Dunbar, Scotland, was regarded as erroneous. No type material exists among Montagu specimens either at the Royal Albert Memorial Museum, Exeter, or The Natural History Museum, London. Furthermore, Montagu's figure (see Figure 50) is equivocal and cannot with confidence be assigned to any *Ctena* species. Nevertheless, Lamy (1920) listed *Venus orbiculata* Montagu as a synonym of the western African species now known as *Ctena eburnea* (Gmelin, 1791). Other names introduced for western Atlantic *Ctena* species (*Lucina occidentalis* Reeve, 1850; *Lucina imbricatula* C. B. Adams, 1845 and variety names for *C. orbiculata* var. *filiata* and var. *recurvata* introduced by Dall (1901)), have usually been placed in synonymy with *C. orbiculata* (Britton, 1971; Bretsky, 1976). The name *Ctena orbiculata* has become firmly entrenched in publications concerning western Atlantic mollusks (e.g. Warmke and Abbott, 1961; Abbott, 1954, 1974; Bretsky, 1976; Vokes and Vokes, 1984; Redfern, 2001; Mikkelsen and Bieler, 2007) and variously classified under other generic and subgeneric combinations of *Codakia* (*Jagonia*), *Codakia* (*Ctena*), or *Codakia* (*Codakia*).

An additional problem arising from ongoing molecular analyses, including our own results (Barnes and Weigt, 1998; Taylor et al., 2011), is that *Ctena orbiculata* is likely a complex of morphologically similar species as have been documented for other western Atlantic bivalves. Certainly, our own results separate *Ctena orbiculata* from the Florida Keys and specimens from Bocas, Panama that on shell characters resemble the type of *Lucina imbricatula* C. B. Adams, 1845, a species that is usually synonymized with *C. orbiculata* (e.g. Bretsky, 1976).

Ctena orbiculata in its varying name combinations is the subject of continuing investigations into the biology of the bacterial symbiosis, host-symbiont relationships (e.g. Giere, 1985; Schweimanns and Felbeck, 1985; Gros et al., 1998; Gros and Felbeck, 2003; Brissac et al., 2009, Gros et al., 2012) and reproductive biology (Bigatti et al., 2004). Because of the biological interest in *Ctena orbiculata*, its abundance in the western Atlantic and the possible existence of sibling species, it has become important to stabilise this well-established name by the designation of a neotype from an appropriate western Atlantic type locality and for which genetic data is available. The International Code of Zoological Nomenclature (ICZN, 1999) specifies (Article 75.3.6) that the neotype should come from a place as near as practicable to the original type locality. In this case, the geographical range of the species lies several thousand kilometres west of the original (likely erroneous) type locality and we have chosen the locality in the Florida Keys because we have published molecular data from a co-occurring, morphologically similar specimen to the neotype.

SYSTEMATICS

Subfamily Codakiinae Iredale, 1937

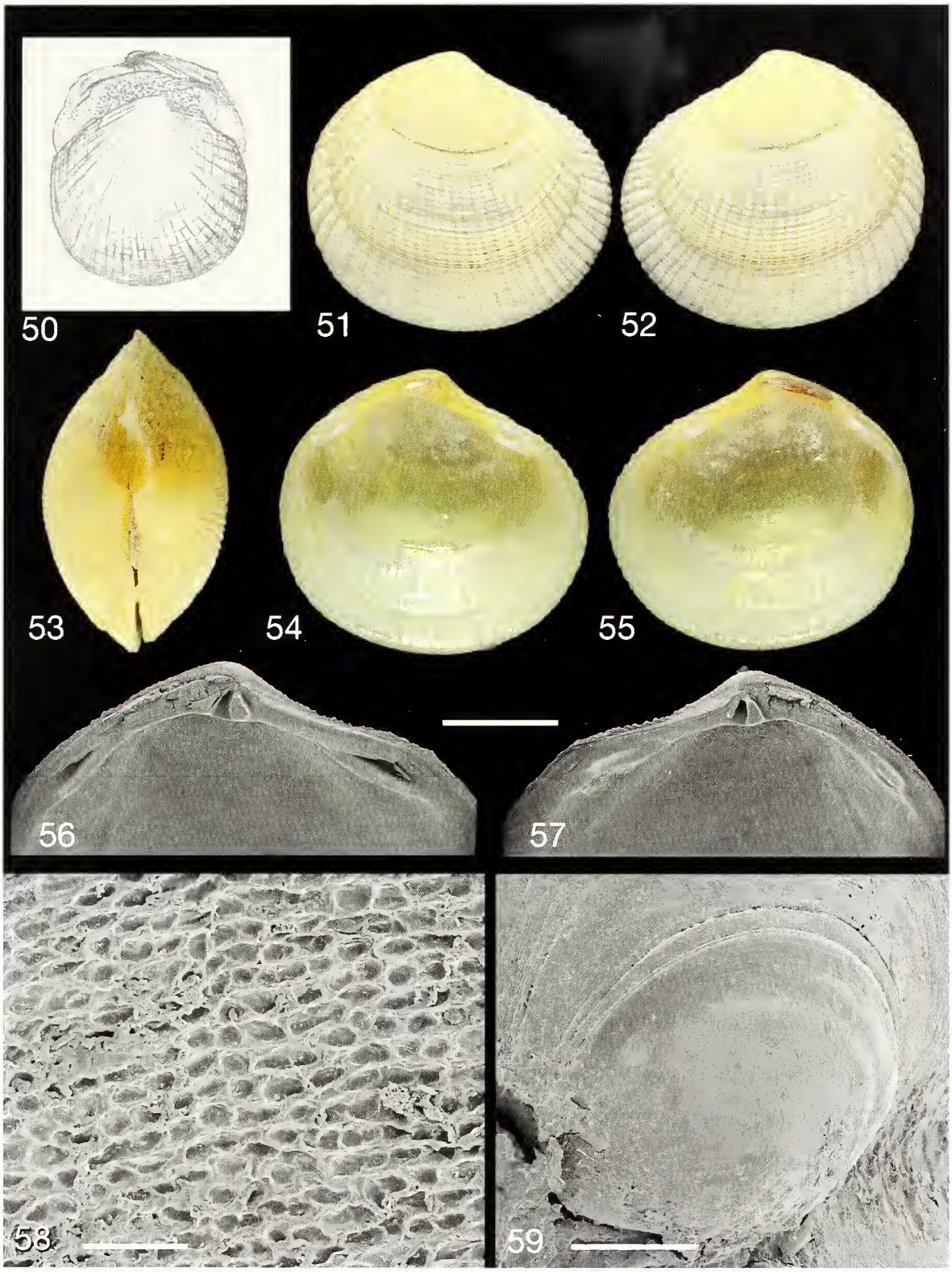
Genus *Ctena* Mörch, 1861

Type Species: *Codakia (Jagonia) mexicana* Dall, 1901, subsequent designation Dall, Bartsch and Rehder, 1938.

***Ctena orbiculata* (Montagu, 1808)**
(Figures 50–59)

Venus orbiculata Montagu, 1808: 42, pl. 29, fig. 7.

Neotype: Whole shell, live-collected, FMNH 339457, collected by G. Bigatti, M. Perhada, J. Taylor and E. Glover during the International Marine Bivalve Workshop 2002, stn. IMBW-FK-622A, 22nd July 2002 (Mikkelsen and Bieler, 2004).



Figures 50–59. *Ctena orbiculata*. **50.** *Venus orbiculata*, copy of original figure from Montagu (1808). **51–55.** Neotype, *Venus orbiculata*, Long Key, FMNH 339457, L=13.6 mm. **51–52.** Exterior of right and left valves. **53.** Dorsal view of conjoined valves. **54–55.** Interior of left and right valves. **56–59.** *Ctena orbiculata*, SEM details of coated specimen from same sample and location as neotype, NHMUK 20130563. **56–57.** Hinge teeth of left and right valves. Scale bar = 2 mm. **58.** Microsculpture. Scale bar = 10 μm. **59.** Protoconch. Scale bar = 50 μm.

Type Locality: USA, Florida Keys, Long Key, bayside, 24°49.5′ N, 80°48.9′ W. 0.5–1.0 m, thin sand over rock platform with *Halodule wrightii*, *Thalassia testudinum*, and *Syringodium filiforme* (Mikkelsen and Bieler, 2004).

Description of Neotype: Shell small, L = 13.6 mm, H = 12.5 mm, T (single valve) = 4.2, longer than high, H/L = 0.92, moderately inflated, T/L = 0.31, exterior and interior pale, yellowish white. Sculpture of many radial ribs (55 at periphery), crossed by fine commarginal lamellae producing scales on summits of ribs. Ribs both divide and intercalate. Prominent major growth halts present. Lunule lanceolate. Ligament short, set in shallow groove. Hinge robust; RV with two cardinal teeth, anteriormost very small, anterior and posterior lateral teeth present, LV with two cardinal teeth, posterior tooth thin, anterior and posterior lateral teeth present. Anterior adductor scar short, broad, detached from pallial line for ½ length at an angle of 15°. Posterior adductor scar reniform. Shell interior within pallial line with radial grooves. Pallial line entire. Inner shell margin denticulate.

Remarks: Details of surface microsculpture and protoconch were examined by SEM on another coated specimen collected with the neotype (NHMUK 20130563). The microsculpture consists of a meshwork of irregular, shallow punctations, ca. 3–6 µm in size (Figure 5B) similar to structures seen in other Codakiinae (Glover and Taylor, in press). The protoconch (Figure 5D) PI+PII= 165 µm, PI=142 µm is irregularly lumpy, PII a narrow rim with fine growth increments.

A specimen (NHMUK 20100254) included in molecular analyses (Taylor et al., 2011) was collected at the same locality and time as the neotype and is very similar in shell characters. GenBank numbers for sequences of three genes: 18S rRNA (AJ 581853), 28S rRNA (AJ581887), cytochrome B (FR686627).

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LITERATURE CITED

Abbott, R.T. 1954. American Seashells. Van Nostrand, New York, 541 pp.

Abbott, R.T. 1974. American Seashells. 2nd edition. Van Nostrand-Reinhold, New York, 663 pp.

Adams, C.B. 1845. Specierum novarum conchyliorum, in Jamaica reportorum, synopsis. Proceedings of the Boston Society of Natural History 2: 1–17.

Allen, J.A. 1958. On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). Philosophical Transactions of the Royal Society of London B241: 421–484.

Barnes, P.A.G. and L.A. Weigt. 1998. Species boundaries within Lucinidae (Bivalvia): application of morphometric and molecular analyses. In: R. Bieler and P.M. Mikkelsen (eds.) Abstracts, World Congress of Malacology, Washington, D.C. 1998. Unitas Malacologica, Chicago, p. 26.

Bigatti, G., M. Peharda, and J. Taylor. 2004. Size at first maturity, oocyte envelopes and external morphology of sperm in three species of Lucinidae (Mollusca: Bivalvia) from Florida Keys, U.S.A. Malacologia 46: 417–426.

Bretsky, S.S. 1976. Evolution and classification of the Lucinidae (Mollusca: Bivalvia). Palaeontographica Americana 8(50): 219–337.

Brissac, T., O. Gros, and H. Mercot. 2009. Lack of endosymbiont release by two Lucinidae (Bivalvia) of the genus *Codakia*: consequences for symbiotic relationships. FEMS Microbiology Ecology 67: 261–267.

Britton, J.C. 1970. The Lucinidae (Mollusca: Bivalvia) of the western Atlantic Ocean. PhD dissertation George Washington University. University Microfilms 71–12, 288.

Britton, J.C. 1972. Two new species and a new subgenus of Lucinidae (Mollusca: Bivalvia), with notes on certain aspects of lucinid phylogeny. Smithsonian Contributions to Zoology 129: 1–19.

Carpenter P.P. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. British Association for the Advancement of Science Report 33: 517–686.

Castresana, J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Molecular Biology and Evolution 17: 540–552.

Chavan, A. 1937. Essai critique de classification des lucines. Journal de Conchyliologie 81: 237–281.

Cleevely, R.J. 1995. Some "malacological pioneers" and their links with the transition of shell-collecting to conchology during the first half of the nineteenth century. Archives of Natural History 22: 385–418.

Conrad, T.A. 1846. Descriptions of new species of fossil and Recent shells and corals. Proceedings of the Academy of Natural Sciences Philadelphia 3: 19–27.

Cosel, R. von and P. Bouchet. 2008. Tropical deep-water lucinids (Mollusca: Bivalvia) from the Indo-Pacific: essentially unknown, but diverse and occasionally gigantic. In: V. Héros, R.H. Cowie and P. Bouchet (eds.) Tropical Deep Sea Benthos 25. Mémoires du Muséum national d'Histoire naturelle 196: 115–213.

Dall, W.H. 1901. Synopsis of the Lucinacea and of the American species. Proceedings of the United States National Museum 23: 779–833.

Dall, W.H. 1903. Contributions to the Tertiary fauna of Florida, with especial reference to the silex-beds of Florida and the Pliocene beds of the Caloosahatchee River. Transactions of the Wagner Free Institute 3 (part 6): 1219–1654.

Dall W.H., P. Bartsch, and H.A. Rehder. 1938. A manual of the Recent and fossil marine pelecypod mollusks of the Hawaiian Islands. Bulletin of the Bernice P. Bishop Museum 153: 1–233.

Dell, R.K. 1964. Antarctic and subantarctic Mollusca: Amphineura, Scaphopoda and Bivalvia. Discovery Reports 33: 93–250.

Distel, D.L. and H. Felbeck, 1987. Endosymbiosis in the lucinid clams *Lucinoma aequizonata*, *Lucinoma annulata* and *Lucina floridana*: a reexamination of the functional morphology of the gills as bacteria-bearing organs. Marine Biology 96: 79–86.

Distel, D.L., H. Felbeck, and C. Cavanaugh. 1994. Evidence for phylogenetic congruence among sulfur-oxidising chemoautotrophic bacterial symbionts and their bivalve host. Journal of Molecular Evolution 38: 533–542.

Fisher, M.R. and S.C. Hand. 1984. Chemoautotrophic symbionts in the bivalve *Lucina floridana* from seagrass beds. Biological Bulletin 167: 445–459.

Fleming, J. 1828. A history of British animals, exhibiting the descriptive characters and systematical arrangement of the genera and species of quadrupeds, birds, reptiles, fishes, Mollusca and Radiata of the United Kingdom; including the indigenous, extirpated and extinct kinds; together with periodical and occasional visitants. Bell & Bradfute, Edinburgh.

Frenkiel, L, and M. Mouëza. 1995. Gill ultrastructure and symbiotic bacteria in *Codakia orbicularis* (Bivalvia, Lucinidae). Zoomorphology 115: 51–61.

Frenkiel, L., O. Gros, and M. Mouëza. 1996. Gill structure in *Lucina pectinata* (Bivalvia: Lucinidae) with reference to hemoglobin in bivalves with symbiotic sulphur-oxidising bacteria. Marine Biology 125: 511–524.

Garcia, E. F. 2000. Surprising new records for Louisiana and the northwestern Gulf of Mexico. American Conchologist 28 (3): 5.

García, E.F. 2008. Molluscan findings from a recent dredging expedition off the Louisiana coast. American Conchologist 36(4): 4–9.

García, E.F. and H.G. Lee. 2002. Report on molluscan species found in the offshore waters of Louisiana, including many extensions of known range and un-named species. American Conchologist 30(4): 10–13.

Garcia, E.F. and H.G. Lee. 2013. Report on molluscan species found in the offshore waters of Louisiana, including many extensions of known range and un-named species. www.jaxshells.org/efg1030.htm

Garfinkle, E.A.R. 2012. A review of North American Recent *Radiolucina* (Bivalvia, Lucinidae) with the description of a new species. ZooKeys 205:19–31.

Gibson-Smith, J. and W. Gibson-Smith. 1982. *Lucina* s.s. (Mollusca: Bivalvia) in the western Atlantic: a reappraisal. The Veliger 25: 139–148.

Giere, O. 1985. Structure and position of bacterial endosymbionts in the gill filaments of Lucinidae from Bermuda (Mollusca, Bivalvia). Zoomorphology 105: 296–301.

Glover, E.A. and J.D. Taylor. 2007. Diversity of chemosymbiotic bivalves on coral reefs: Lucinidae of New Caledonia and Lifou (Mollusca, Bivalvia). Zoosystema 29: 109–181.

Glover, E.A. and J.D. Taylor. In Press. Lucinidae of the Philippines: highest known diversity and ubiquity of chemosymbiotic bivalves from intertidal to bathyal depths (Mollusca: Bivalvia: Lucinidae). Mémoires du Museum national d'Histoire Naturelle.

Glover, E.A., J.D. Taylor, and A.A. Rowden. 2004. *Bathyaustriella thionipta*, a new lucinid bivalve from a hydrothermal vent on the Kermadec Ridge, New Zealand and its relationship to shallow-water taxa (Bivalvia: Lucinidae). Journal of Molluscan Studies 70: 283–295.

Gmelin, J.F. 1791. Caroli a Linné systema naturae per regna tria naturae. 13th edition volume 1, part 6 Vermes, pp. 3021–3910.

Gros, O, L. Frenkiel, and M. Mouëza. 1998. Gill filament differentiation and experimental colonization by symbiotic bacteria in aposymbiotic juveniles of *Codakia orbicularis* (Bivalvia: Lucinidae). Invertebrate Reproduction and Development 34: 219–231.

Gros, O., P. Durand, L. Frenkiel, and M. Mouëza. 1998. Putative environmental transmission of sulfur-oxidizing gill endosymbionts in four tropical lucinid bivalves, inhabiting various environments. FEMS Microbiology Letters 160: 257–262.

Gros, O., N.H. Elisabeth, S.D.D. Gustave, A. Caro, and N. Dubilier. 2012. Plasticity of symbiont acquisition throughout the life cycle of the shallow-water tropical lucinid *Codakia orbiculata* (Mollusca: Bivalvia). Environmental Microbiology 14: 1584–1595.

Gros, O., M. Liberge, and H. Felbeck. 2003. Interspecific infection of aposymbiotic juveniles of *Codakia orbicularis* by various tropical lucinid gill-endosymbionts. Marine Biology 142: 57–66.

Hauser, I., W. Oschmann, and E. Gischler. 2007. Modern bivalve assemblages on three atolls offshore Belize (Central America, Caribbean Sea). Facies 53: 451–478.

Heide, T. van der, L.L. Govers, J. de Fouw, H. Olff, M. van der Geest, M.M. van Katwijk,, T., Piersma, J. van de Koppel, B.R., Silliman, A.J.P. Smolders, and J.A. van Gils. 2012. A three-stage symbiosis forms the foundation of seagrass ecosystems. Science 336: 1432–1434.

Huelsenbeck, J.P., and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754–755.

ICZN (International Commission on Zoological Nomenclature), 1999. International Code of Zoological Nomenclature. International Trust for Zoological Nomenclature, London, 306 pp.

Iredale, T. 1937. The Middleton and Elizabeth Reefs, South Pacific Ocean. Mollusca. Australian Zoologist 8: 232–261.

Jackson, J.B.C., 1972. The ecology of molluscs of *Thalassia* communities, Jamaica, West Indies. II. Molluscan population variability along an environmental stress gradient. Marine Biology 14: 304–337.

Jackson, J.B.C. 1973. The ecology of molluscs of *Thalassia* communities, Jamaica, West Indies. I. Distribution, environmental physiology, and ecology of common shallow-water species. Bulletin of Marine Science 23: 313–350.

Jensen, R.H. and T.A. Pearce. 2009. Marine mollusks of Bermuda. Delaware Museum of Natural History, Wilmington, 473 pp.

Katoh, K., K. Misawa, K. Kuma, and T. Miyata. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research 30: 3059–3066.

Lamy, E. 1920. Révision des Lucinacea vivants du Museum d'Histoire Naturelle de Paris. Journal de Conchyliologie 65: 71–388.

Lee, T. and D.Ó Foighil. 2005. Placing the Floridian marine genetic disjunction into a regional evolutionary context using the scorched mussel, *Brachiodontes exustus*, species complex. Evolution 59: 2139–2158.

McMillan, N.F. 1971 Three lamellibranchs apparently new to Britain. Journal of Conchology 27: 266.

Marko, P.B. and A.L. Moran. 2009. Out of sight, out of mind: high cryptic diversity obscures the identities and histories of geminate species in the marine bivalve subgenus *Acar*. Journal of Biogeography 36: 1861–1880.

Mikkelsen, P.M. and R. Bieler. 2004. International Marine Bivalve Workshop 2002: introduction and summary. Malacologia 46: 241–248.

Mikkelsen, P.M. and R. Bieler. 2007. Seashells of Southern Florida. Living marine mollusks of the Florida Keys and adjacent regions. Bivalves. Princeton University Press, Princeton, New Jersey, 503 pp.

Montagu, G. 1808. Testacea Britannica, Supplement. London 183 pp, pls 17–20.

Mörch, O.A.L. 1861. Beiträge zur Molluskenfauna Central-Amerika's. Malacozoologische Blätter 7: 171–213.

Oliver, P.G., H. Wood, and A.M. Holmes. 2009. First British record of the shipworm *Uperotus* (Bivalvia: Teredinidae) from driftwood on the Llyn Peninsula, Wales. Journal of Conchology 39: 681–682.

d'Orbigny, A. 1834–1847. Voyage dans l'Amérique Méridionale. Exécuté pendant les Années 1826– 1833. Volume 5 Mollusques. Paris Bertrand, Paris & Levrault, Strasbourg. 758 pp. (pp. 529–600 published 1846).

d'Orbigny, A. 1842–1853. Mollusques. In: R. de la Sagra. Histoire Physique, Politique, et Naturelle de l'Ile de Cuba. Volume 2 Bertrand, Paris, 380 pp. (pp. 225–380, pls 26–28 published 1853, see Mikkelsen and Bieler, 2007: 451

Parker, R.H. and J.R. Curray. 1956. Fauna and bathymetry of banks on continental shelf, northwest Gulf of Mexico. Bulletin of the American Association of Petroleum Geologists 40: 2428–2439.

Philippi, R.A. 1848–1850. Abbildungen und Beschriebungen neuer oder wenig gekannter Conchylien 3, Theodor Fischer, Cassel, 138 pp.

Récluz, C. A. 1869. Mélanges malacologiques: II. Monographie du genre *Jagonia* Récluz, 1853. Actes de la Société Linnéenne de Bordeaux 1869: 35–41.

Redfern, C. 2001. Bahamian Seashells; a Thousand Species from Abaco, Bahamas. Boca Raton, Florida, 280 pp., 124 pls.

Reeve, L. A., 1850. Monograph of the genus *Lucina* Pls V–XI. Conchologica Iconica, Volume 6., Reeve, Benham & Reeve, London.

Rios, E. C. 1994. Seashells of Brazil. 2nd edition. Fundação Universidade do Rio Grande, Museu Oceanográfico, Rio Grande, 368 pp.

Sacco F. 1901. I molluschi de terreni terziarii del Piemonte e della Liguria. Part 29. C. Clausen, Torino, 216 pp.

Schweimanns, M. and H. Felbeck. 1985. Significance of the occurrence of chemoautotrophic bacterial endosymbionts in lucinid clams from Bermuda. Marine Ecology–Progress Series 24: 113–120.

Taylor J.D. and E.A. Glover. 2006. Lucinidae – the most diverse group of chemosymbiotic molluscs. Zoological Journal of the Linnean Society 148: 421–438.

Taylor, J.D. and E.A. Glover. 2009. New lucinid bivalves from hydrocarbon seeps of the western Atlantic (Mollusca: Bivalvia: Lucinidae). Steenstrupia 30: 127–140.

Taylor, J.D. and E.A. Glover. 2013. New lucinid bivalves from shallow and deeper water of the Indo-West Pacific Oceans (Mollusca: Bivalvia: Lucinidae). ZooKeys 326: 69–90.

Taylor, J.D., E.A. Glover, L. Smith, P. Dyal, and S.T. Williams. 2011. Molecular phylogeny and classification of the chemosymbiotic bivalve family Lucinidae (Mollusca: Bivalvia). Zoological Journal of the Linnean Society 163: 15–49.

Turgeon, D.D., W.G. Lyons, P.M. Mikkelsen, G. Rosenberg, and F. Moretzsohn. 2009. Bivalvia (Mollusca) of the Gulf of Mexico. In: D.L Felder and D.K. Camp (eds.) Gulf of Mexico — Origins, Waters and biota. Biodiversity. Texas A&M University Press, College Station, Texas, pp. 711–744.

Tunnell, J.W., J. Andrews, N.C. Barrera, and F. Moretzsohn. 2010. Encyclopedia of Texas Shells. Texas A&M University Press, College Station, Texas, 512 pp.

Verrill, A.E. and K.J. Bush. 1900. Additions to the marine Mollusca of the Bermudas. Transactions of the Connecticut Academy of Sciences 10: 513–545.

Vokes, H.E. and E.H. Vokes. 1984. Distribution of shallow-water marine Mollusca, Yucatan Peninsula, Mexico. Mesoamerican Ecology Institute Monograph 1. Middle American Research Institute Publication 54, 183 pp., 50 pls.

Warmke, G.L. and R.T. Abbott, 1961. Caribbean Seashells. Dover Publications, New York, 346 pp.

Weisbord, N.E. 1964. Late Cenozoic pelecypods from northern Venezuela. Bulletins of American Paleontology 45(204): 1–564.

Williams, S.T. 2012. Advances in molecular systematics of the gastropod superfamily Trochoidea. Zoologica Scripta 41: 571–595.

Woodring, W.P. 1925. Contributions to the geology and palaeontology of the West Indies. Miocene molluscs from Bowden, Jamaica. Pelecypods and scaphopods. Carnegie Institute Washington Publication 366: 1–222, 28 pls.

Extractrix dockeryi, a new species from the Eocene of the southeastern United States, with notes on open coiling in the Cancellariidae (Gastropoda: Neogastropoda)

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ABSTRACT

Extractrix dockeryi is described from beds of Middle Eocene (Bartonian) age in the Gosport Sand Formation at Little Stave Creek, Alabama and the contemporaneous McBean Formation at Orangeburg, South Carolina. This new species represents the earliest occurrence of open coiling in the family Cancellariidae. Other records of open coiling in the Cancellariidae are reviewed, and the taxonomic status and composition of the genus *Extractrix* is discussed.

Additional Keywords: Cancellariidae, *Extractrix*, open coiling, Eocene

INTRODUCTION

We report the discovery of a new species of open-coiled cancellariid from two different Middle Eocene (Bartonian) deposits in the southeastern United States, one, the Gosport Sand Formation at Little Stave Creek, Alabama, the other, the McBean Formation at Orangeburg, South Carolina. This new species represents the earliest known occurrence of open coiling in the family Cancellariidae. It is assigned to the genus *Extractrix* Korobkov, 1955, based on similarities to its type species, *Extractrix extractrix* (Boettger, 1906), from Middle Miocene (Badenian) deposits of the Transylvanian Basin in Romania (Lăpugiu de Sus). We review the literature for other records of whorl detachment in the Cancellariidae, and discuss the taxonomic status and composition of the genus *Extractrix*.

OCCURRENCE OF OPEN COILING IN CANCELLARIIDAE

Whorl detachment, the lack of contact between successive whorls of a coiled shell, is rare among gastropods. The degree and regularity of whorl detachment may vary considerably, from simple detachment of portions of the final whorl, as in *Valvata sincera ontariensis* Baker, 1931 (see Clarke, 1973: 225, pl. 20, figs. 8,9) to the occurrence of multiple detached and loosely or irregularly coiled whorls, as in *Tenagodus squamatus* (Blainville, 1827) (see Abbott and Dance, 1982: 61, as *Siliquaria squamata*). We follow Yochelson, (1971: 236) in applying the term "disjunct" to forms that have a detached last whorl; "uncoiled" to forms in which coiling is very irregular; and "open-coiled" to forms in which the whorls are detached, yet coiling conforms closely to a logarithmic spiral.

The prevalence of whorl detachment within particular gastropod taxa may also vary. Disjunct, uncoiled and open-coiled forms of whorl detachment may occur as unique or rare events in normally coiled species, either as teratalogical or gerontic (Yochelson, 1971: 236) conditions, or as a malformation following unsuccessful predation involving shell breakage. Whorl detachment may also occur more widely in predominantly tightly coiled taxa [e.g., in *Spirolaxis rotulacatherinea* (Melvill and Standen, 1903), see Bieler, 1993:325, figs. 268-270; or in *Valvata juliae* Scholz and Glaubrecht, 2010, (their fig. 2 documents frequencies of open coiling of up to 25% in various populations)]. Detached whorls may also become a fixed character of a species or subspecies. Rex and Boss (1976) reviewed the incidence of such open-coiling in Recent gastropods and reported that it occurs at very low frequency ($\approx 7.5 \times 10^{-4}$). Among the examples they documented, 26.7% were planispiral species in which open coiling was due primarily to increases in the distance of successive whorls from the axis of coiling [high values of D, according to the terminology of Raup's (1961, 1966) model of shell coiling]. For the majority of taxa (60.0%), open coiling was a consequence of elongation of the shell along the axis of coiling [high whorl translation rate, T (Raup, 1961; 1966)], while 13.3% of the taxa were open-coiled according to both criteria. In some instances, open coiling appears to be sufficiently

adaptive to have given rise to diversified open-coiled lineages [e.g., *Cycloscala* Dall, 1889 (Epitoniidae); *Eccliseogyra* Dall, 1892 (Nystiellidae) ; *Extractrix* Korobkov, 1955 (Cancellariidae)].

Known instances of whorl detachment within the family Cancellariidae are listed in Table 1. *Extractrix extractrix*, *E. dockeryi* new species, and *E.milleri* (Burch, 1949) all show a marked increase in the degree of elongation (increase in the whorl translation rate, T) at the protoconch / teleoconch transition, resulting in open coiling for all teleoconch whorls (only the first 0–½ teleoconch whorls are in contact with prior whorls). Although Janssen (1984a: 21) considered *Trigonostoma protrigonostoma* Sacco, 1894 to be closely related to *Extractrix extractrix*, the former has a shell (Sacco, 1894: pl. 1, figs. 3a,3b) that more closely resembles *Trigonostoma umbilicare* (Brocchi, 1814), differing from that species in having a portion of the body whorl (~ ½ whorl) disjunct. In contrast, the early teleoconch whorls of *Trigonostoma* ("*Extractrix*") *hoerlei* Olsson, 1967 are nearly planispiral, with the increase in the elongation rate occurring in the second teleoconch whorl (Figure 23, arrow), resulting in a shell in which only the last 1–1½ whorls are disjunct. There is a report (Coucom, 1975) of a single disjunct specimen of *Trigonostoma scalare*, a species that is normally coiled, in which the last ½ whorl is detached.

SYSTEMATICS

Family Cancellariidae Forbes and Hanley, 1851
Subfamily Cancellariinae Forbes and Hanley, 1851

Genus *Extractrix* Korobkov, 1955

Pseudomalaxis (*Extractrix*) Korobkov, 1955:138. Type species: *Pseudomalaxis extractrix* (Boettger, 1906) by original designation.
Trigonostoma (*Extractrix*) Olsson, 1967:23-24.

Diagnosis: Shell small to medium-sized (to 27 mm), with tall, conispiral, deeply umbilicate, open-coiled shell. Protoconch of smooth, evenly rounded whorls. Transition to teleoconch marked by major increase in degree of elongation along the axis of shell coiling, resulting in loss of contact between whorls within first ½ teleoconch whorl. Teleoconch of up to 4 whorls, sharply triangular in cross-section. Carinae along shoulder and siphonal canal with open spines (long to barely discernible).

Remarks: The type species of *Extractrix* was described as *Discohelix* (*Pseudomalaxis*) *extractrix*, in the family Architectonicidae by Boettger (1906: 138), and retained in this family by subsequent authors (e.g., Cossmann, 1916; Zilch, 1934), including Korobkov (1955), who proposed *Extractrix* as a subgenus of *Pseudomalaxis*. Citing Boettger's (1906: 138) reference to two small columellar plaits, Olsson (1967:23) transferred *Extractrix* to the family Cancellariidae, as a subgenus of *Trigonostoma*, but regarded it as a "form genus" and questioned the relationship of its type species to other loosely coiled cancellariids. Janssen (1984a: 20) treated the type species as belonging to *Trigonostoma sensu stricto*, and considered it to be closely related to *Trigonostoma protrigonostoma* Sacco, 1894, a species in which only a portion of the body whorl is disjunct. Harzhauser and Landau (2012: 56) regarded the status of the genus *Extractrix* as questionable. They considered the species assigned to this genus to form a morphological group based on open coiling that was not necessarily monophyletic, but possibly an assemblage of independently evolved, uncoiled species of *Trigonostoma*.

Prior authors have assigned cancellariid species to the genus *Extractrix* primarily, if not exclusively on the basis of the presence of either disjunct whorls or open coiling, an approach that has rendered this genus paraphyletic. The updated diagnosis of *Extractrix* is based on more precisely defined shell characters that are shared by the type species and some, but not all cancellariid species with disjunct or open coiled shells. We conclude that these characters are sufficient to define a clade that is related to *Trigonostoma*, but has persisted from the

Table 1. Records of whorl detachment within the family Cancellariidae.

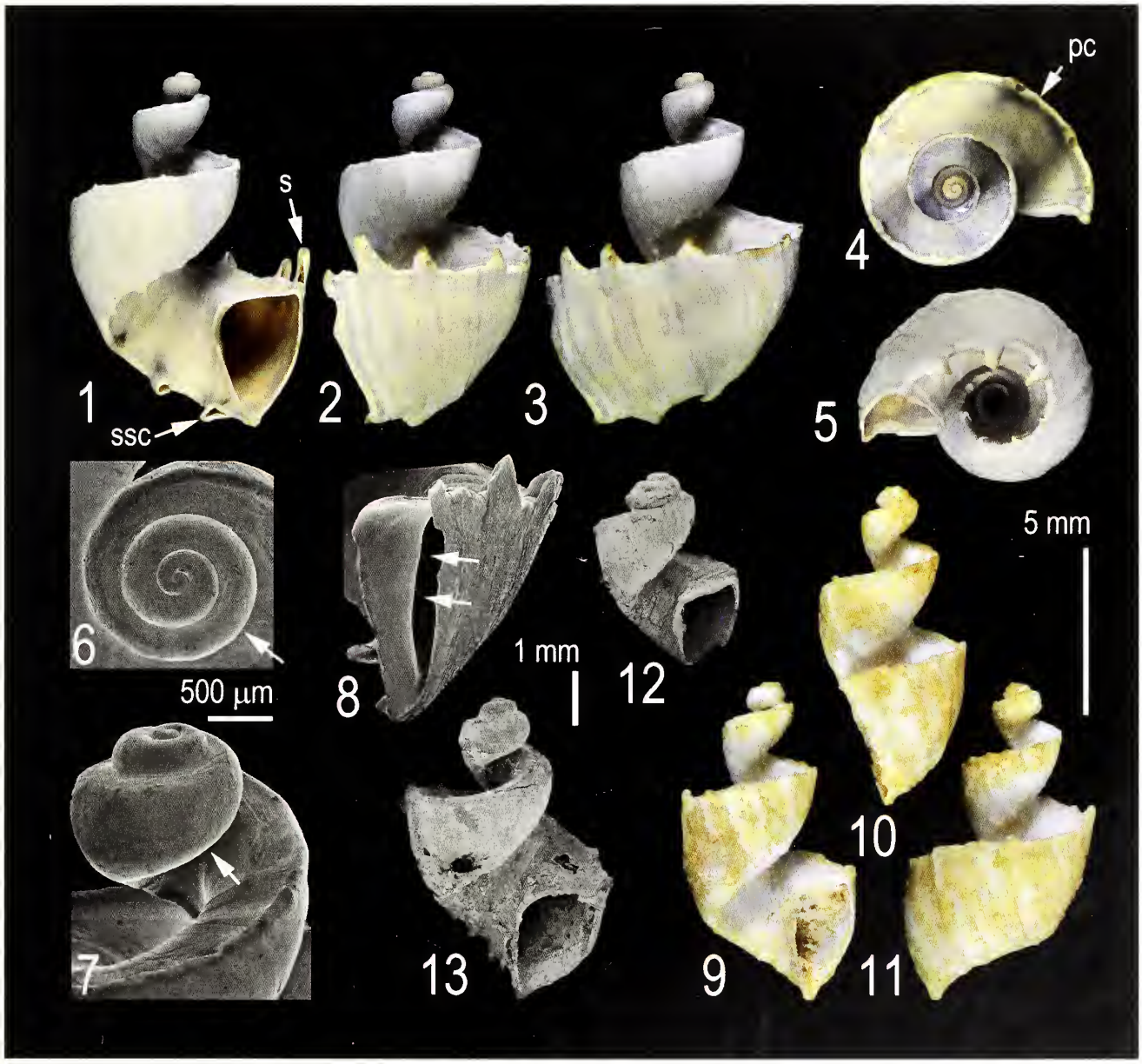
Taxon	Age	Geographic Range	Coiling Type	No. of known specimens[1]
Extractrix dockeryi new species	Eocene	SE USA	Open	4
Extractrix extractrix (Boettger, 1906)	Miocene	S + E Europe	Open	4+?
?*Extractrix* cf. *extractrix* Janssen, 1984a,b[2]	Miocene	N Europe	Open	35
Extractrix milleri (Burch, 1949)	Pleistocene-Recent[3]	E Pacific Galapagos[3]	Open	>50
Trigonostoma protrigonostoma Sacco, 1894	Miocene	Europe	Disjunct (~ last ½ whorl)	1+?
Trigonostoma hoerlei Olsson, 1967	Pliocene	E USA + Caribbean[4]	Disjunct (last whorl)	> 6
Trigonostoma scalare Gmelin, 1791	Recent	Indo-Pacific	Disjunct[5] (~ last ½ whorl)	1

[1] Number of specimens with detached whorls reported in the literature.
[2] Harzhauser and Landau (2012:56) suggested that the specimens from the Netherlands reported by Janssen (1984a,b) represent a species different from *E. extractrix*.
[3] Landau *et al.* (2012:223)
[4] Jung (1977) reported this species from the early Pliocene Punta Gavilán Formation of coastal Venezuela.
[5] Coucom (1975)

Eocene to the Recent, with records in the eastern Pacific [Pleistocene-Recent], southeastern United States [Eocene] and northern and eastern Europe [Miocene].

***Extractrix dockeryi* new species**
(Figures 1–13)

Description: Shell (Figures 1–13) small (to 10.7 mm) thin, with tall, narrow (spire angle 51–66°), conispiral, deeply umbilicate, open-coiled shell. Protoconch (Figures 6, 7) increasing in diameter from 83 µm to 1.09 mm in 2¾ smooth, evenly rounded whorls, deviated from teleoconch axis by ~9°. Transition to teleoconch distinct, marked by slight change in surface texture and curvature (Figures 6, 7, arrows), as well as a major increase in the degree of elongation along the coiling axis of the shell [rate of whorl translation, T (Raup, 1966) increasing from ~1.5 for the protoconch to ~3.25 for



Figures 1–13. *Extractrix dockeryi* new species. **1–8.** Holotype, UF 242210, Little Stave Creek, Alabama. **1.** Apertural. **2.** Lateral, **3.** Dorsal, **4.** Apical, and **5.** Umbilical views of the shell. **6.** Apical and **7.** Lateral views of the protoconch. Arrows indicate transition from protoconch to teleoconch. **8.** Columella. Arrows indicate vestiges of columellar folds. **9–11.** Paratype 1, Petit Collection 3488, about 3 miles WNW of Orangeburg, Orangeburg County, South Carolina. **12–13.** Paratypes 2 and 3. FMNH 328571, Edge of Caw Caw Swamp, WNW of Orangeburg, Orangeburg County, South Carolina. 5 mm scale bar applies to Figures 1–5 and 9–11; 500 µm scale bar applies to Figures 6, 7; 1 mm scale bar applies to Figures 8, 12, 13. Abbreviations: **pc**, peripheral carina; **s**, shoulder spines; **ssc**, siphonal canal spines.

teleoconch] that results in none of the teleoconch whorls being in contact with each other. Teleoconch with up to 2½ sharply shouldered whorls that are strongly triangular in cross section. The adabical portion of each whorl is flat, tabulate, nearly perpendicular to coiling axis (forming an angle of 70–82°), the abaxial margin is demarcated by a sharply angled shoulder with a weak peripheral carina (Figure 4, pc) bearing broad, open spines. Outer portion of each whorl weakly convex, sinuate and recurved at juncture with short siphonal canal. Columellar portion of each whorl straight, nearly parallel to coiling axis in early whorls (Figures 12, 13), angle increasing up to 22° in later whorls (Figure 1). Outer portion of whorl and columella form an acute angle (30–39°), bearing a carina along their juncture, while the juncture of the columella and the adapical region is evenly rounded. Spiral sculpture absent or limited to barely perceptible, extremely fine spiral threads on portions of the outer surface of the last whorl. Axial sculpture of simple, weak, prosocline, growth striae, raised, open spines (Figure 1, s) along shoulder (8–11 on last whorl), and weaker, adaxially deflected open spines (Figure 1, ssc) along the carina at the anterior edge of the siphonal canal (0–7 on last whorl). Spines on shoulder and siphonal canal may be prominent or weak and worn. Aperture triangular, with short, pronounced siphonal canal. Outer lip smooth, columella with two very weak columellar folds (Figure 8, arrows).

Type Material: Holotype, Florida Museum of Natural History, University of Florida, UF 242210; Paratype 1, Petit Collection 3488, About 3 miles WNW of Orangeburg, Orangeburg County, South Carolina, [McBean Formation, Middle Eocene (Bartonian)]; Paratypes 2-3. The Field Museum, FMNH 328571, Edge of Caw Caw Swamp, WNW of Orangeburg, Orangeburg County, South Carolina [McBean Formation, Middle Eocene (Bartonian)].

Type Locality: Little Stave Creek, Clarke County, Alabama [Gosport Sand Formation, Claiborne Group, Middle Eocene (Bartonian)].

Distribution and Habitat: This species is presently known from the type locality as well as from the McBean Formation, WNW of Orangeburg, South Carolina. Both deposits are of Middle Eocene (Bartonian) age. The sand deposits at the type locality were "probably laid down in less than 20 fathoms [36.6 m] of water" (Gardner, 1957: 584). The Orangeburg Sand of the McBean Formation correlates with the Gosport Sand (Dockery et al., 1992) and was also deposited on a shallow marine shelf, mainly in low energy conditions (Nystrom et al., 1991).

Etymology: This new species honors Dr. David T. Dockery III, of the Office of Geology, Mississippi Department of Geology and Environmental Quality, in recognition of his many contributions to the study of the Tertiary paleontology of Alabama and Mississippi.

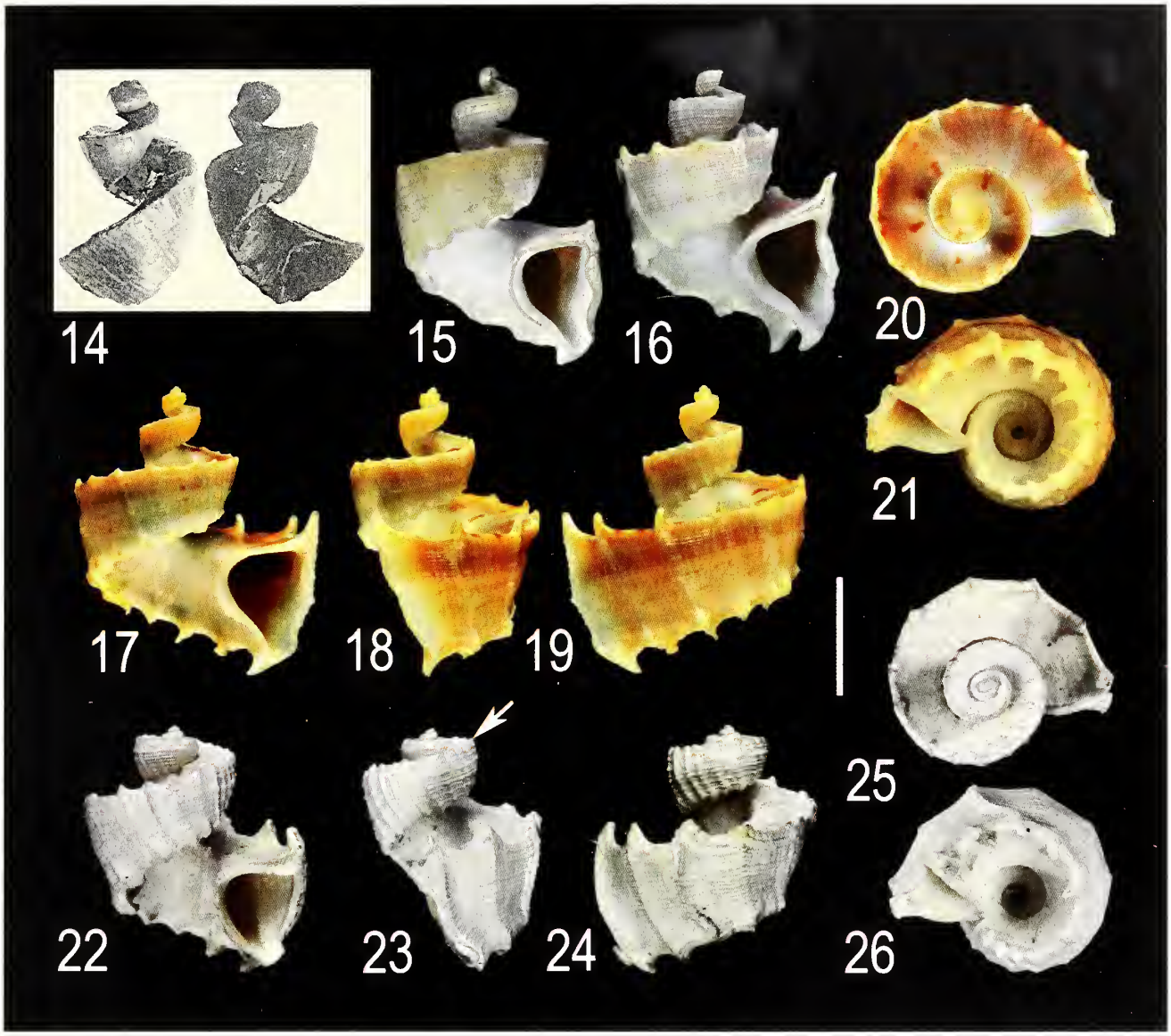
Comparative Remarks: This new species most closely resembles *Extractrix extractrix* (Boettger, 1906), the type species of the genus *Extractrix* Korobkov, 1955 (Figure 14), a Miocene species that has been reported from the Burdigalian-Langhian of Romania (Boettger, 1906) and the Netherlands (Janssen, 1984a,b) as well as from the Messinian of Italy (Davoli, 1995). Both species have open-coiled shells in which teleoconch whorls are not in contact due to high rates of whorl translation (T = 3.0–3.8), sharply triangular whorl profiles, and lack pronounced spiral sculptural elements. *Extractrix dockeryi* new species differs from *E. extractrix* in having proportionally broader, more inflated whorls, and pronounced carinae along the shoulder, and at the end of the short, constricted siphonal canal. The presence of open spines distinguishes *E. dockeryi* from Romanian and Italian specimens of *E. extractrix*, but specimens from the Netherlands may have low spines along both carinae that may be connected by weak axial ridges (Janssen, 1984a: pl. 2, fig. 16; 1984b: pl.66, figs. 6,7). Harzhauser and Landau (2012: 56) suggested that the specimens from the Netherlands represent a species different from *E. extractrix*. *Extractrix dockeryi* is easily distinguished from its Pleistocene-Recent congener, *E. milleri* (Burch, 1949) (Figures 15-21), a species from the tropical eastern Pacific that has a much larger (to 26 mm), broader shell with axial and spiral sculpture.

DISCUSSION

As more rigorously defined, the genus *Extractrix* contains its type species *Extractrix extractrix* from the Miocene of Europe, *E. dockeryi* new species from the Eocene of the southeastern United States, and *Extractrix milleri* from the Pleistocene-Recent of the tropical eastern Pacific. In the event that the specimens from the Miocene of the Netherlands that had been attributed to *E. extractrix* by Janssen (1984a, b) are segregated as a separate species, as suggested by Harzhauser and Landau (2012), this too should be included in *Extractrix*. Both "*Trigonostoma*" *hoerlei* and "*Trigonostoma*" *protrigonostoma* are excluded from *Extractrix* as both have disjunct rather than open coiled shells. The relationship of *T. hoerlei* (Figures 22–26) appears closer to some species of *Ventrilia*, suggesting an independent origin of whorl detachment.

The genus *Extractrix* appears to have originated in the western Atlantic during the Eocene and spread eastward to Europe, where widespread populations (North Sea, Paratethys and Tethys Basins) were present during the Miocene. It survives in the Recent fauna as a paciphile genus, which once inhabited the western Tertiary Caribbean Province, but is now presumably extinct there and survives in eastern Pacific waters (Woodring, 1966: 426).

Open coiling is generally regarded as maladaptive as it increases vulnerability to shell breaking predators and impedes mobility, but may survive in situations where such ecological limitations are relaxed (e.g., when



Figures 14–26. *Extractrix* species. **14.** *Extractrix extractrix* (Boettger, 1906). Lectotype, Lăpugiu de Sus, Romania (Specimen lost, see Harzhauser and Landau, 2012: 56. Figures from Cossmann 1916: pl. 12, figs. 25–26). **15–21.** *Extractrix milleri* (Burch, 1949). **15.** Apertural view of Holotype USNM 600660, Near Punta Arenas, Tambor, Costa Rica. **16.** Apertural view of USNM 679301, Guaymas, Mexico. **17.** Apertural, **18.** Lateral, **19.** Dorsal, **20.** Apical and **21.** Umbilical views of shell. Petit Collection 2397, Arenas de Quebro, Panama, in 73 m. **22–26.** *Trigonostoma* ("*Extractrix*") *hoerlei* Olsson, 1967. Holotype, USNM 645162, Kissimmee, Florida. **22.** Apertural, **23.** Lateral, **24.** Dorsal, **25.** Apical and **26.** Umbilical views of shell. Scale bar = 3 mm for figure 14; = 1 cm for Figures 15–21; = 1.5 cm for Figures 22–26.

populations expand following a calamity, or when a previously unoccupied or temporarily favorable environment is colonized) (Vermeij, 1987: 42).

Disjunct coiling in *Valvata juliae*, for example, was limited to a short stratigraphic interval within the Pleistocene, and believed to be a response to high levels of environmental stress caused by lake level fluctuations in the Lake Turkana (Scholz and Glaubrecht, 2010).

Rex and Boss (1973) conceded that the selective significance of open coiling is unclear, and recognized that it evolved independently in several unrelated lineages to fill "dissimilar environmental roles." They noted the success of some open-coiled taxa in terms of broad geographic distributions and/or their persistence through geological time. Several lineages with open-coiled shells (e.g., genera within Epitoniidae, Nystiellidae, Architectonicidae) are known to be ectoparasites of cnidarians. Cancellariids are characterized by an alimentary system highly specialized for suctorial feeding on body fluids (Harasewych and Petit, 1998). Depending on species, prey organisms range from sharks and rays (O'Sullivan et al., 1987) to bivalves and gastropods (Loch, 1987).

No cancellariid species have yet been reported to feed on cnidarians. When the habitat and diet of *Extractrix milleri* is better known, it may shed insights on the advantages open coiling bestows on species of the genus *Extractrix*, a lineage that has persisted from the Eocene to the Recent.

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LITERATURE CITED

Abbott, R.T. and S.P. Dance. 1982. Compendium of Seashells. E.P. Dutton, New York, 414 pp.

Bieler R. 1993. Architectonicidae of the Indo-Pacific (Mollusca, Gastropoda). Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 30: 1–376.

Boettger, O. 1906. Zur Kenntnis der Fauna der mittelmiocänen-Schichten von Kostejin Krassó-Szörényer Komitat. III. (Gastropoden und Anneliden). Verhandlungen und Mitteilungen des siebenbürgischenVereins für Naturwissenschaften zu Hermannstadt, 54/55, i-iii, 1-244.

Burch, J.Q. 1949. A new *Trigonostoma* from Central America. Minutes of the Conchological Club of Southern California 94: 2–4.

Clarke, A.H. 1973. The freshwater molluscs of the Canadian Interior Basin. Malacologia 13: 1–509.

Cossmann, A.M. 1916. Essais de Paléoconchologie comparée. 10. Privately published, Paris, 292 pp., 12 pls.

Coucom, E. 1975. Cancellaria? Keppel Bay Tidings, 13(5): 8.

Davoli, F. 1995. I molluschi del Messiniano di Borelli (Torino). 3. Cancellariidae. Bollettino del Museo Regionale de Scienze Naturali Torino 13: 221–264.

Dockery, D.T. III and P.G. Nystrom, Jr. 1992. The Orangeburg District molluscan fauna of the McBean Formation: a new, diverse silicified fauna within the *Glyptoactis* (*Claibornicardia*) *alticostata* zone above the occurrence of *Cubitostrea sellaeformis*, an interval zone of Gosport age. Proceedings of the Second Bald Head Island Conference on Coastal Plains Geology, Hilton Head Island, November 6–11, 1990, pp. 90–96.

Gardner, J. 1957. Little Stave Creek, Alabama–Paleoecologic Study. In: Ladd, H.S. (ed.) Treatise on Marine Ecology and Paleoecology 2. Geological Society of America Memoir 67. New York, pp. 573–587.

Harasewych, M.G. and R.E. Petit. 1998. Superfamily Cancellarioidea. In: Beesley, P.L., G.J.B., Ross, and A. Wells (eds.) Mollusca: The Southern Synthesis. Fauna of Australia 5B. CSIRO Publishing, Melbourne, pp. 845–846.

Harzhauser, M. and B. Landau. 2012. A revision of the Neogene cancellariid gastropods of the Paratethys Sea. Zootaxa 3472: 1–71.

Janssen, A.W. 1984a. An account of the Cancellariidae (Gastropoda) of Winterswijk-Miste (Miocene, Hemmoorian), The Netherlands. Scripta Geologica 68: 1–39, pls. 1–6.

Janssen, A.E. 1984b. Mollusken uit het Mioceen van Winterswijk-Miste. Koninklijke Nederlandse Naturhistorische Vereniging, Nederlands Geologische Vereniging, Rijksmuseum van Geologie en Mineralogie, Amsterdam, 451 pp., 82 pls.

Jung, P. 1977. Two rare gastropod genera from the Pliocene of Venezuela. Eclogae Geologicae Helvetiae 70: 845–854.

Korobkov, I.A. 1955. Spravochnik i methodicheskoe rukovodstvopo tretichnym molljuskam. Briukonogie. [Reference and methodological guide to Tertiary mollusks. Gastropoda]. Gostopteckhizdat, Leningrad, 795 pp., 117 pls.

Landau, B., R.E. Petit, W. Etter and C.M. da Silva. 2012. New species and records of Cancellariinae (Caenogastropoda) from tropical America, together with a catalogue of Neogene to Recent species from this region Cainozoic Research 9: 193–279.

Loch, I. 1987. Man bites dog. Australian Shell News 59–60: 9.

Nystrom, P.G. Jr., R.H. Willoughby and L.K. Price. 1991. Cretaceous and Tertiary Stratigraphy of the Upper Coastal Plain, South Carolina (In:) Horton, J.W. Jr. and V.A. Zullo (eds.) The Geology of the Carolinas: Carolina Geological Society Fiftieth Anniversary Volume. University of Tennessee Press, Knoxville, pp. 221–240.

Olsson, A.A. 1967. Some Tertiary Mollusks from South Florida and the Caribbean. Paleontological Research Institution, Ithaca, 61 pp., 9 pls.

O'Sullivan, J.B., R.R. McConnaughey and M.E. Huber. 1987. A blood-sucking snail: the Cooper's nutmeg, *Cancellaria cooperi* Gabb, parasitizes the California Electric Ray *Torpedo californica* Ayres. Biological Bulletin 172: 362-366.

Raup, D.M. 1961. The geometry of coiling in gastropods. Proceedings of the National Academy of Sciences 47: 602–609.

Raup, D.M. 1966. Geometric analysis of shell coiling: general problems. Journal of Paleontology 40: 1178–1190.

Rex, M.A. and K.J. Boss. 1976. Open coiling in recent gastropods. Malacologia 15: 289–297.

Sacco, F. 1904. I molluschi dei terrei terziarii del Piemonte e della Liguria. Pt. 16. (Cancellariidae). C. Clausen, Torino, 78 pp. 3 pls.

Scholz, H. and M. Glaubrecht. 2010. A new and open coiled *Valvata* (Gastropoda) from the Pliocene Koobi Fora Formation of the Turkana Basin, Northern Kenya. Journal of Paleontology 84: 996–1002.

Vermeij, G.J. 1987. Evolution and Escalation: An Ecological History of Life. Princeton University Press, New Jersey, 527 pp.

Woodring, W.P. 1966. The Panama land bridge as a sea barrier. Proceedings of the American Philosophical Society 110: 425–433.

Yochelson, E.L. 1971. A new Late Devonian gastropod and its bearing on problems of open coiling and septation. In: Dutro, J.T.J. (ed.) Paleozoic perspectives: a paleontological tribute to G. Arthur Cooper. Smithsonian Contribution to Paleobiology 3: 231–241.

Zilch, A. 1934. Zur Fauna des Mittel–Miocäns von Kostej (Banat). Typus Bestimmung und Tafeln zu O. Boettger's Bearbeitungen. Senckenbergiana, 16: 193–302, 22 pls.

A new land snail of the genus *Eucalodium* from Belize (Gastropoda: Pulmonata: Urocoptoidea: Eucalodiidae)

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ABSTRACT

Eucalodium belizensis new species is described from Belize. It is the first species of the genus reported from there.

Additional Keywords: Gastropods, land snails, Central America

INTRODUCTION

The subgenus *Eucalodium* is known from mountainous terrains in a rather small area of Belize, Guatemala, and part of Mexico (northern Chiapas and Tabasco.) *Eucalodium* species of are seldom encountered, and they are not common where they are found. This is the first species of the genus and the subgenus reported from Belize. The species is described prior to a review of the genus *Eucalodium* by the senior author.

MEASUREMENTS

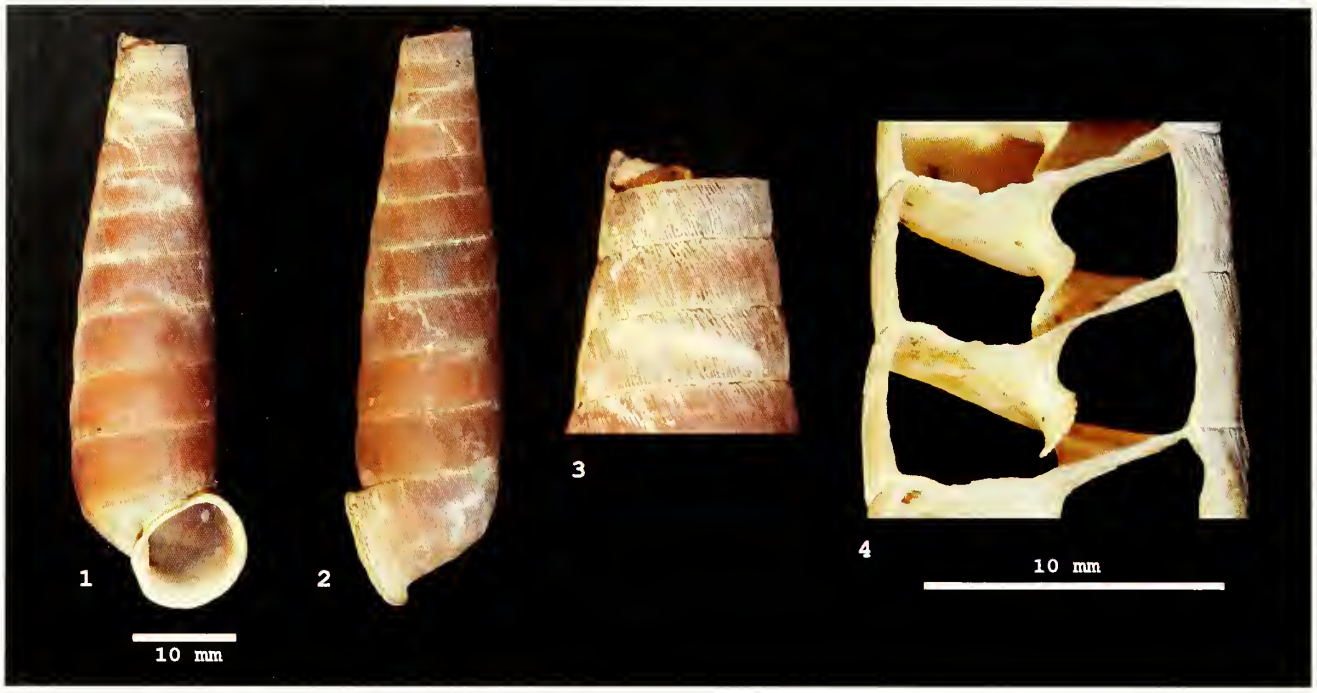
The length of adult shell is measured from the top of the apical plug to the base of the aperture. The width of the shell is perpendicular to the axis, but does not include the aperture. The apex is the whorl at the apical plug. The following abbreviations are used in the text: AH = height of aperture; AW = width of aperture; ApexW = width of apical whorl; SL = standard length; SW = standard width.

Eucalodium (*Eucalodium*) *belizensis* new species

Figures 1–4

Diagnosis: The shell is purple-brown. It is decollated, solid, and thick-walled, about 51–57 mm long, and includes 9.4–11.8 whorls below the apical plug. The aperture is broadly ovate in shape. The columella is strongly twisted, producing a flattened, crenulated lamella. The uniformly tapered spire is nearly straight-sided. The sculpture consists of distinct riblets on the upper 4-5 whorls. The riblets are less distinct or obsolete on the lower half of the shell, and then again become distinct on last whorl.

Description: The solid thick-walled shell is purple-brown with a lighter colored base and with a white peristome (Figure 1). It is moderately large, attaining a length of about 51–57 mm below the apical plug, 14.4–15.0 mm standard width, 0.25–0.28 times as wide as long. The aperture is about 0.71–0.85 times the shell width. The shell is decollate and contains 9.4–11.8 whorls. The apical whorl is 7.0–7.8 mm wide, and is 0.48–0.52 times the standard shell width. The whorls are nearly flat with a shallow suture. The spire is slightly concave in profile along the earlier whorls and is slightly convex below. The apical plug is oblique and nearly flat. The base of the last whorl is rounded with an obsolete circum-basal cord. The imperforate umbilicus is marked by a narrow indentation. The sculpture consists of numerous oblique, slightly sigmoid, sharp thread-riblets. The riblets are most distinct on the upper whorls where they are about as wide as their interspaces, and are slightly higher than wide (Figure 3). The riblets are less defined and distinct on the lower part of the spire, and then again become more distinct on the last whorl. In one paratype they are distinct nearly through the length of the spire. The holotype has 96 riblets on the penultimate whorl. A paratype (UF 448722b) has 106 riblets. The aperture projects forward slightly in lateral profile (Figure 2), and is oblique, lying at an angle of about 20–21° to the shell axis (21 in holotype). It is broadly ovate in shape with an obtuse posterior corner. The parietal margin is weakly convex. The peristome is narrowly reflected and rounded. The peristome is widest along the palatal and basal margins, and is narrowest along the parietal margin. A columellar fold extends down and forward to the peristome. The internal axis is strongly twisted, producing a flattened spiral lamella that is crenulated along its edge (Figure 4). The lamella extends for about 0.1 of the distance across the cavity of the whorl. The crenulated nodes on the lamella are most developed in the penultimate and anti-penultimate whorls.



Figures 1–4. *Eucalodium belizensis* new species. **1–3.** Holotype (UF 449720). **4.** Paratype (UF449722).

Type Material: Holotype: UF 449720, April 2010. Paratypes: UF 449721 (one specimen), April 2010; UF 449722 (2 specimens), April 2012. All type material from type locality and collected by Valentino Tzub.

Three paratypes are available. Two (UF 449721, UF 449722b) are bleached and worn specimens in which the sculpture is no longer clearly evident. The third paratype (UF 444922b) retains the periostracum and the sculpture. It differs from other paratypes and the holotype by having a relatively wider aperture in which the columellar lamella is stronger and distorts the columellar lip. Standard measurements of type material are given in Table 1.

Type Locality: Belize, Toledo District, 5.5 km north of San José; 2 km northeast of Miramar Hill (16.335° N, 89.114° W), 650 m altitude.

The type locality is reached by the Southern Highway about 8 km from the intersection of the road to Punta Gorda, and right (north) on a paved road, past Crique Jute for about 33 km to the village of San José. The type locality is approximately 5.5 km due north on a trail from San José.

The collector, Valentino Tzub, is a Kek'chi Mayan from the village of San José who occasionally works as a guide and research assistant for scientific expeditions and research projects in Belize.

Habitat: Specimens were found under leaf litter near Cretaceous limestone outcrops. The landform surrounding the type locality includes hilly karst topography, containing sinkholes and multiple cave formations. The type locality is entirely forested with a tropical wet broadleaf evergreen forest with cohune palms (*Attalia cohune*) and occasional emergent tree (*Ceiba*) and with an understory layer dominated with shrubs, pteridophytes, and Araceae. Farming activity from San Jose is encroaching into the near-by forest.

Table 1. Measurements in mm of type material of *Eucalodium belizensis* new species.

	SL	SW	ApexW	AH	AW	Whorls
Holotype	57.3	14.4	7.2	11.8	11.2	10.6
Paratypes						
UF444921	51.3	14.4	7.0	11.4	10.2	9.3
UF444922a	57+	14.7	7.1	—	—	11.3
UF444922b	53.3	15.0	7.8	11.5	12.4	9.4

DISCUSSION

Eucalodium belizensis is the first record of the genus *Eucalodium* in Belize. *Eucalodium* Fischer and Crosse, 1868 includes four subgenera: *Eucalodium* s.s., *Oligostylus* Pilsbry, 1895, *Resupinata* Martens, 1897, and *Ptychocentrum* Bartsch, 1943 (Thompson, 2011). *Oligostylus* and *Resupinata* are distinguished from *Eucalodium* s.s. by lacking an internal lamella on the axis, and by having thin-walled shells with a brownish periostracum. The generic affinity of *Ptychocentrum* is problematic. It has an internal lamella similar to that in species of the subgenus *Eucalodium*, but the lamella is not crenulated, and the axis is hollow, approaching that

of *Coelocentrum* species. Its shell is thick-walled and is chestnut-brown in color.

The subgenus *Eucalodium* is known for certain from a rather small area of northern Chiapas, Tabasco (both in Mexico), Guatemala, and Belize. Formerly the subgenus must have been generally distributed and common within this area, but deforestation has extirpated it from much of its former range. Records from there are few. Species are seldom encountered, and they are not common where they are found. The paucity of specimens in museum collections makes taxonomic study difficult. All locality records for the subgenus *Eucalodium* lie north of the North American-Central American Continental Divide in the Polochíc Valley of Guatemala-Chiapas. *Oligostylus* is more widespread, ranging from Jalisco, Mexico south to El Salvador (Thompson, 1963). *Resupinata* is found from San Luís Potosí south the Veracruz. *Ptychocentrum* is known from a single locality in Chiapas.

The subgenus *Eucalodium* includes *E. compactum* Pilsbry, 1893, *E. decollatum decollatum* (Nyst, 1841), *E. d. guatemalensis* (Bartsch, 1906, *E. otoides* Thompson, 1968, and *E. mexicanum* (Pfeiffer, 1860). The species are medium sized to large and have a strongly twisted axis that forms a flattened spiral lamella, which may be crenulated along it edge (as in Figure 4). *Eucalodium d. decollatum* is known only from small area near Teapa, Tabasco (Thompson, 2011). *Eucalodium decollatum guatemalensis* is reported from an unspecified locality in Guatemala (Bartsch, 1906). *Eucalodium otoides* is known from a single locality in northern Chiapas, and *E. compactum* is known from an unspecified locality in Tabasco. Pfeiffer (1860) described *E. mexicanum* from an unspecified locality in Mexico. Fischer and Crosse (1873) record a variety of *E. (Eucalodium) mexicanum* from between Tactíc and Tamahú, Dept. Alta Verapaz, Guatemala, and they record two forms of *E. mexicanum* from Juquila, Oaxaca. Their records concerning the distribution of *E. mexicanum* appear unlikely because of the wide geographic separations.

Eucalodium belizensis is similar in size to *E. compactum*, which differs from *E. belizeusis* by having weaker, more widely spaced sculpture, a concave parietal margin in the aperture, and a thinner, light-brown shell. *Eucalodium otoides* differs from *E. bezensis* by having fewer whorls below the apical plug (7.6–7.9) and by having an auriform aperture with a straight parietal margin, a strongly reflected and twisted columellar margin that forms an obtuse angle with the basil margin, and a more robust shell that is 0.31-0.32 times as wide as long. *Eucalodium decollatum* is a large, robust species. Shells are 64–74 mm in length, and 0.28–0.31 times as wide as long. The sculpture consists of poorly defined oblique riblets that are nearly obsolete over most of the shell. There are about 75–86 obsolete riblets discernible along he suture on the penultimate whorl. *Eucalodium decollatum guatemalensis* is similar in length and whorl count to *E. belizensis*, except that it is more robust, being 17.5 mm wide at the penultimate whorl, and it has a smooth, not crenulated, columellar lamella. *Eucalodium mexicanum* differs from *E. belizensis* by having a thin-walled shell that is light brown in color.

ACKNOWLEDGMENTS

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LITERATURE CITED

Bartsch, P. 1906. The urocoptid mollusks from the mainland of America in the collection of the United States National Museum. Proceedings of the United States National Museum 31: 100–160.

Bartsch, P. 1943. A new subgenus and species of *Coelocentrum*. The Nautilus 56: 91–92.

Fischer, P. and H. Crosse. 1870–1878. Mission Scientifique au Mexique et dans L'Amerique Centrale. Études sur les mollusques terrestres et fluviatiles du Mexique et du Guatemala, 1. Paris, 702 pp.

Martens, E. v. 1890–1901. Biologia Centrali-Americana. Mollusca. British Mnseum (Natnral History), 706 pp.

Nyst, H. 1841. Notices sur deux Cochilles Mexicaines appartenant aur genres *Pupa* et *Helix*. Buletin de l'Académie Royal de Bruxelles 8: 343.

Pfeiffer, L. 1860. Descriptions of thirty-six new species of land shells from Mr. H. Cuming's collection. Proceedings of the Zoological Society of London 1860: 133–141.

Pilsbry, H.A. 1893a. Notes on a collection of shells from the state of Tabasco, Mexico. Proceedings of the Academy of Natural Science of Philadelphia 44: 338–341.

Pilsbry, H.A. 1902–1903. Manual of Conchology: Urocoptidae. Ser. 2, Vol. 15. Academy of Natural Sciences, Philadelphia, 323 pp.

Strebel, H. and G. Pfeffer. 1880. Beitrag zur Kenntniss der Fauna mexikanischer Land- und Süsswasser-Conchylien. Teil IV. Hamburg, J. J. Kerbst, 122 pp., pls. 15 pls.

Thompson, F.G. 1963. New land snails from El Salvador. Proceedings of the Biological Society of Washington 76: 19–32.

Thompson, F.G. 1968a. Some Mexican land snails of the family Urocoptidae. Bulletin of the Florida State Museum 12: 125–183; fig. 1–29.

Thompson F.G. 2011. An annotated checklist and bibliography of the land and freshwater snails of México and Central America. Bulletin of the Florida Museum of Natural History 50: 1–299.

Determination of EC_{50} for normal oyster larval development in extracts from bloom-forming green seaweeds

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ABSTRACT

Blooms of ulvoid algae can decimate marine ecosystems, outcompeting seagrasses and other habitat-forming species and directly killing animals due either to the production of allelochemicals or various effects (e.g., anoxia) associated with bloom mortality. Oyster larvae (*Crassostrea gigas*) are susceptible to extracts from dried ulvoids at relatively low concentrations. Here we determine a specific EC_{50} for extracts from the bloom-forming species *Ulva lactuca* and *Ulvaria obscura*. The EC_{50} for *Ulva* is equivalent to 0.13 gfm·L^{-1} while the value for *Ulvaria* is 0.21 gfm·L^{-1}. Assuming moderate bloom conditions, these data suggest that an EC_{50} could be achieved in 5,200 to 8,500 L of seawater for each m^2 of algal bloom. Possible mechanisms for developmental toxicity include the breakdown products of DMSP (in both species), dopamine quinones (in *Ulvaria* only), or as yet unidentified toxins.

Additional Keywords: Crassostrea gigas, *Ulvaria obscura*, *Ulva lactuca*, Allelopathy, Harmful Algal Blooms

INTRODUCTION

So-called "green tides" (blooms of green macroalgae) have been increasing worldwide causing problems ranging from anoxia to direct overgrowth of valuable marine plant communities (Valiela et al., 1997, Hauxwell et al., 2000). The organisms causing green tides are predominantly ulvoid macroalgae (Family Ulvaceae), though other species may be responsible (e.g., Lapointe et al. 2005).

Mass mortality of fish and bivalves coincident with macroalgal blooms have been reported in Sweden (Rosenberg et al., 1990). Their effects have directly altered human activities as well, e.g., causing concerns with sailing events during the 2008 Olympic Games and the death of domestic animals (Anonymous, 2009). In Washington State, USA, the public has been alarmed by bloom-induced anoxia creating potentially dangerous H_2S concentrations in residential neighborhoods. Local blooms are sufficient to negatively impact eelgrass growth (Nelson and Lee, 2001).

Specifically allelopathic impacts of ulvoid algae have been noted or suggested occasionally in the past. Extracts from *Ulva* spp. are thought to inhibit larval development in barnacles, crab, flounder, and mosquitoes (Magre, 1974; Johnson, 1980; Johnson and Welsh, 1985; Thangam and Kathiresan, 1991, Walters et al., 1996, Borowsky et al., 1997). Nelson et al. (2003a) have demonstrated that crude, water-soluble extracts from two bloom forming species (*Ulva lactuca* L., 1753 and *Ulvaria obscura* [Kützing] Gayral, 1969) inhibit normal development of oyster (*Crassostrea gigas* Thunberg, 1793) zygotes. Here we determine the concentration of extracts from two common "green tide" seaweeds (*U. lactuca* and *U. obscura*) that result in a 50% decline in normal oyster zygote development through the D-hinge stage (EC_{50}).

MATERIALS AND METHODS

Algae were collected from Seattle, Washington, USA (47°32.4′ N, 122°23.8′ W). Algal disks (9 cm diameter, approximately 0.7 gfm per disk) were dried for 30 min outdoors in the shade, effectively killing the alga. Dried disks were placed in microwave-sterilized seawater for 90 min at a ratio of one disk per 50 mL of seawater (or ~14 gfm·L^{-1}). This yielded what we estimated to be the maximum concentration of extract that organisms encounter in the field and is scaled to 100% hereafter. The concentration is equivalent to a volume of seawater 5 cm deep covering the densest portion of a heavy bloom of ulvoid algae (i.e. ~six algal thalli thick, as observed by the authors and reported in terms of mass by Nelson et al., 2003b).

EC_{50} for oyster embryo larval development was determined following standard techniques (ASTM, 1989, described fully in Nelson et al., 2003a). The study was conducted during late July to correspond with the natural gamete maturation in oysters. Oysters were

hand-spawned and aliquots of sperm were added to egg suspension to achieve a ratio of 10–20 sperm per egg. Within 1 h of fertilization, the embryo suspension was transferred into test chambers (polystyrene Coulter counter vials).

For *Ulvaria*, we tested concentrations of 0%, 0.1%, 0.3%, 0.6%, 1.6%, and 3.9%. For *Ulva*, we tested concentrations of 0.5%, 0.9%, 1.5%, 2.7%, and 4.7%. Each treatment dilution had 7 (*Ulva*, at 2.7%) or 8 (all others) replicates. Filtered seawater was used for seawater controls, stock solutions, and dilutions. The test chambers were maintained at 25°C for 24 h. Temperature and $[O_2]$ of a separate container of seawater were checked every 4–6 h as a proxy for the incubation vials containing oyster larvae. Larvae were fixed with 1 mL of formaldehyde added to each vial after 24 hours. All larvae in each test chamber were identified as normal or abnormal based on their development to the D-hinge stage.

EC_{50} of *Ulva* and *Ulvaria* extracts were determined by fitting a non-linear regression as follows:

$$Y = B + (T - B)/(1 + (X/EC_{50})^{(H)}) \quad \text{(Equation 1)},$$

where X is the concentration tested, Y is the fraction of the larvae that developed normally, B represents the lowest possible proportion surviving, T represents the

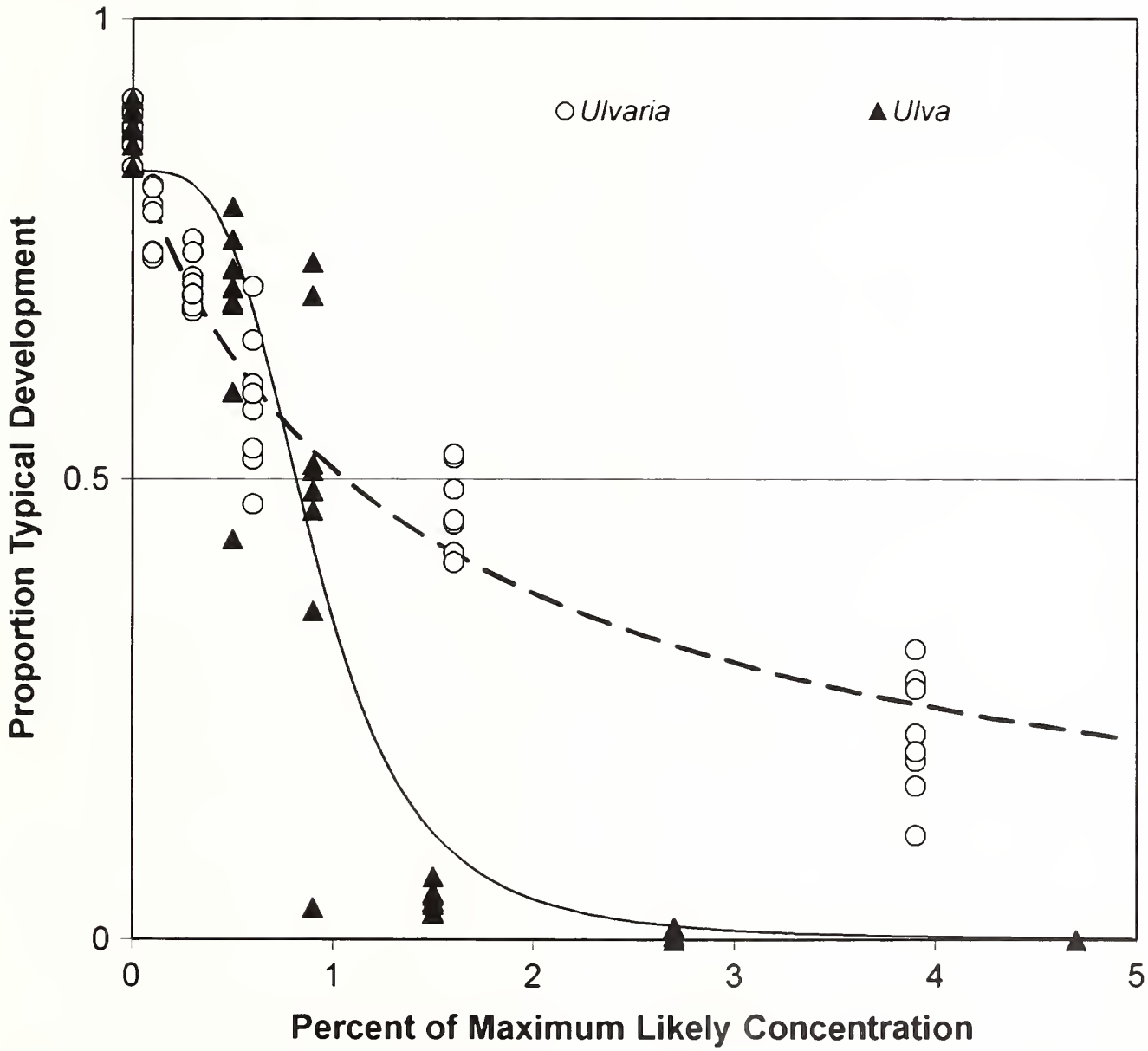

Figure 1. The fraction of oyster larvae developing to the D-hinge stage in various concentrations of extracts from *Ulva lactuca* and *Ulvaria obscura*. Best-fit curves are shown for *U. lactuca* (solid line) and *U. obscura* (dashed line) based on the Equation 1 where $Y = (0+(0.867-0))/(1 + ([\text{Ulvaria extract}]/1.494\%)^{0.906})$ and $Y = (0+(0.835-0))/(1 + ([U.\ lactuca\ \text{extract}]/0.910\%)^{3.654})$.

highest possible proportion surviving, and H is the Hill coefficient. Constraints were placed on T and B (0<= B<=0.5 and 0.5<=T<=1.0).

RESULTS

Regressions for both *Ulva* and *Ulvaria* extract concentration versus oyster larval success were significant (Figure, $F_{1,43}$=2.956, p=0.0304; and $F_{4,44}$=4.982, p =0.002; respectively) and explained over 90% of the variation in larval success (R^2=0.911 and 0.942, respectively, Figure). EC_{50} for *Ulva* was 0.91±0.054% and for *Ulvaria* 1.5±0.70% (means±SE). The means are equivalent to 0.13 and 0.21 gfm·L^{-1}, respectively for *Ulva* and *Ulvaria* tissue.

Given a moderately dense bloom has 200 gdm·m^{-2} (Nelson et al., 2003b), the fm:dm ratio in these algae is approximately 1:0.182, and the EC_{50} values reported here, the death of the bloom would release sufficient toxin to create EC_{50} concentrations in 5,200 (for *Ulvaria*) to 8,500 (for *Ulva*) L·m^{-2} of bloom area.

DISCUSSION

Oyster developmental failure may be attributable to one of several toxins found in ulvoid algae. Both *Ulva* and *Ulvaria* spp. have been shown to contain nontoxic dimethylsulfoniopropionate which breaks down spontaneously or enzymatically to form the toxins dimethyl sulfide and acrylate (Van Alstyne et al., 2001; Van Alstyne and Houser, 2003; Erickson et al., 2006; Lyons et al., 2007). *Ulvaria obscura* contains dopamine, which oxidizes in solution (Tocher and Craigie, 1966, Graham et al., 1978) to form reactive oxygen species (ROS) and dopamine quinone. The quinone has both cytotoxic and genotoxic effects (Stokes et al., 1999). ROS can damage lipids, proteins, and DNA (Halliwell and Gutteridge, 1989; Lesser, 2006). Larval crab (*Cancer* spp.) survival is significantly reduced when zoeae are exposed to dopamine at environmentally relevant concentrations (Harvey, 2007).

Further, it is possible that an unidentified toxin or other cause is at play. Some authors suggest that fatty acids may be involved. *Ulva linza* L., 1753 produces an approximately 400 Da lipid that inhibits *Fucus distichus* L., 1767 germination (K. Van Alstyne, pers. comm.). Wang et al. (2011) cite the work of Fusetani et al. (1976) on the icthyotoxic properties of lipids produced by the green alga *Chaetomorpha minima* F.S.Collins and Hervey, 1917 and suggest that *Ulva* spp. may be similarly toxic. Wang et al. (2011) found that juvenile abalone (*Haliotis discus hannai* Ino, *1953*) were susceptible to toxins from media in which living or decomposing *Ulva prolifera* O. F. Müller, 1778 had been steeped. Both were toxic with LC_{50} between 12–15 gfm·L^{-1} algal tissue, with a slight but significantly greater effect of decomposing tissues. The authors suggest that allelochemicals produced by either the living or decomposing algae contribute to mortality, with increased mortality caused by decomposition-induced hypoxia as well as release of sulfides and ammonia.

Release of these compounds and the toxic impacts of crude extracts are associated with death of the algal tissue, particularly when induced by desiccation (Nelson et al., 2003a, Van Alstyne et al., 2011). *Ulvaria* is less desiccation tolerant than *Ulva*, thus likely to release toxins following a shorter drying period (Nelson et al., 2010). A flooding tide on a hot day would create EC_{50} or higher conditions in 1,000's of L of seawater per m^2, potentially impacting organisms on nearby shorelines.

Toxicity of green algal extracts to oyster larvae is particularly problematic in an era of increasing bloom intensity and frequency. Losses in the larval stages could limit the success of commercially grown and wild oyster populations. Negative consequences are magnified by the greater sensitivity of oyster larvae: The EC_{50} determined here is between 1 and 2 orders of magnitude lower than most previously tested algal and animal model systems (Nelson et al., 2003a, Harvey, 2007, Wang et al., 2011). If toxic impacts are occurring primarily at cell surfaces, algal cell walls and multicellular animal shells or exoskeletons may limit the impacts and could account for differences in toxic impacts noted for various species.

Algal bloom management practices should be informed by the possible negative impact on oyster larvae. In Washington State, USA, past practices have included seining of green algae off beaches followed by their release in mid-channel. While appreciated by beachfront property owners, this practice simply moves toxins to another location. In China, dried green algal tissue has been proposed as a remedy for red tides (Jin et al., 2005). While effective in limiting dinoflagellate population growth, the potential for this "cure" harming species it is intended to protect should be evaluated.

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LITERATURE CITED

Anonymous. 2009. Lorry driver 'first human casualty' of toxic seaweed fumes. The Times (London). September 8, 2009, p. 41.

ASTM. 1989. Standard guide for conducting static acute toxicity test starting with embryos of four species of saltwater bivalve mollusks. American Society for Testing and Materials, Philadelphia, PA, (ASTM) E724–89: 334–51.

Borowsky, R. and B. Borowsky. 1990. Feeding inhibition of the salt marsh amphipod *Gammarus palustris* Bousfield, 1969 by heat-labile substances in *Ulva lactuca* L. Crustaceana 59: 299–301.

Erickson, A., V. Paul, K. Van Alstyne, and L. Kwiatkowski. 2006. Palatability of macroalgae that use different types of chemical defenses. Journal of Chemical Ecoogy. 32: 1883–1895.

Fusetani, N., C. Ozawa, and Y. Hashimoto. 1976. Fatty acids as ichthyotoxic constituents of a green alga *Chaetomorpha minima*. Bulletin of the Japanese Society of Scientific Fisheries 42: 941.

Graham, D., S. Tiffany, W.J. Bell, and W. Gutknecht. 1978. Autoxidation versus covalent binding of quinones as the mechanism of toxicity of dopamine, 6–hydroxydopamine, and related compounds toward C1300 neuroblastoma cells *in vitro*. Molecular Pharmacology 14: 644–653.

Halliwell, B and J. Gutteridge. 1989. Free radicals in biology and medicine. Oxford University Press, Oxford, 704 pp.

Hauxwell, J., J. Cebrian, C. Furlong, and I. Valiela. 2000. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. Ecology 82: 1007–1022.

Harvey, E.L. 2007. The Effects of Ulvoid Macroalgae on the Settlement of Crab Megalopae and Survival and Growth of Juvenile Crabs. MS Thesis, Western Washington University, Bellingham, Washington, USA. 64 pp.

Jin, Q., S. Dong, and C. Wang. 2005. Allelopathic growth inhibition of *Prorocentrum micans* (Dinophyta) by *Ulva pertusa* and *Ulva linza* (Chlorophyta) in laboratory cultures. European Journal of Phycology 40: 31–37.

Johnson, D. 1980. Effects of phytoplankton and macroalgae on larval and juvenile winter flounder (*Pseudopleuronectes americana* Walbaum) cultures. MS Thesis, University of Rhode Island, Kingston, Rhode Island, 61 pp.

Johnson, D. and B. Welsh. 1985. Detrimental effects of *Ulva lactuca* (L.) exudates and low oxygen on estuarine crab larvae. Journal of Experimental Marine Biology and Ecology 86: 73–83.

Lapointe, B.E., P.J. Barile, M.M. Littler, D.S. Littler, B.J. Bedford, and C. Gasque. 2005. Macroalgal blooms on southeast Florida coral reefs: 1. Nutrient stoichiometry of the invasive green alga *Codium isthmocladum* in the wider Caribbean indicates nutrient enrichment. Harmful Algae 4: 1092–1105.

Lesser, M. 2006. Oxidative stress in marine environments: biochemistry and physiological ecology. Annual Review of Physiology 68: 253–278.

Lyons, D., K.L. Van Alstyne, and R. Scheibling. 2007. Antigrazing activity and seasonal variation of dimethylsulfoniopropionate-associated compounds in the invasive alga *Codium fragile* ssp. *tomentosoides*. Marine Biology 153: 179–188.

Magre, E.J. 1974. *Ulva lactuca* L. negatively affects *Balanus balanoides* (L.) (Cirripedia Thoracica) in tidepools. Crustaceana 27: 231–234.

Nelson, T.A. and A. Lee. 2001. A manipulative experiment demonstrates that blooms of the macroalga *Ulvaria obscura* can reduce eelgrass shoot density. Aquatic Botany 71: 149–154.

Nelson, T.A., D. Lee and B.C. Smith. 2003a. Toxic extracts from ulvoid macroalgae: Are "green tides" harmful algal blooms? Journal of Phycology 39(5): 874– 879.

Nelson, T.A., A.V. Nelson and M. Tjoelker. 2003b. Seasonal patterns in ulvoid algal biomass, productivity, and key environmental factors in the Northeast Pacific. Botanica Marina 46: 263–275.

Nelson, T.A., J. Olson, L. Imhoff, and A.V. Nelson. 2010. Aerial exposure and desiccation tolerances are correlated to species composition in "green tides" of the Salish Sea (northeastern Pacific). Botanica Marina 53: 103–111.

Rosenberg, R., R. Elmgren., S. Fleischer, P. Jonsson, G. Persson, and H. Dahlin. 1990. Marine eutrophication case studies in Sweden. Ambio 19: 102–108.

Stokes, A., T. Hastings, K. Vrana. 1999. Cytotoxic and genotoxic potential of dopamine. Journal of Neuroscience Research 55: 659–665.

Thangam, T. and K. Kathiresan. 1991. Mosquito larvicidal effect of seaweed extracts. Botanica Marina 34: 433–435.

Tocher, R.D. and J.S. Craigie. 1966. Enzymes of marine algae: II. Isolation and identification of 3 hydroxytyramine as the phenolase substrate in *Monostroma fuscum*. Canadian Journal of Botany 44: 605–608.

Valiela, I., J. McClelland, J. Hauxwell, P.J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. Limnology and Oceanography 42: 1105–1118.

Van Alstyne, K.L., L.T. Houser. 2003. Dimethylsulfide release during macroinvertebrate grazing and its role as an activated chemical defense. Marine Ecology Progress Series 250: 175–181.

Van Alstyne, K.L., G. V. Wolfe, T. L. Freidenburg, A. Neill and C. Hicken. 2001. Activated defense systems in marine macroalgae: evidence for an ecological role for DMSP cleavage. Marine Ecology Progress Series 213: 53–65.

Van Alstyne, K.L., K.J. Anderson, A.K. Winans and S.A. Gifford. 2011. Dopamine release by the green alga *Ulvaria obscura* after simulated immersion by incoming tides. Marine Biology 158: 2087–2094.

Walters, L.J., M.G. Hadfield, and C.M. Smith. 1996. Waterborne chemical compounds in tropical macroalgae: positive and negative cues for larval settlement. Marine Biology 126: 382–392.

Wang, C., R. Yu, and M. Zhou. 2011. Acute toxicity of live and decomposing green alga *Ulva* (*Enteromorpha*) *prolifera* to abalone *Haliotis discus hannai*. Chinese Journal of Oceanology and Limnology 29: 541–546.

Research Note

Intaglicollonia, a new name for the Eocene gastropod *Nehalemia* Hickman, 1974 (Gastropoda: Coloniidae)

Intaglicollonia is proposed as a replacement name for the monotypic Eocene gastropod genus *Nehalemia* Hickman, 1974, family Colloniidae Cossmann, 1916. The type species, *Nehalemia hieroglyphica* Hickman, 1974, was based on 11 specimens from a siltstone unit at the top of the Cowlitz Formation in Washington County, northwestern Oregon (early late Eocene). The siltstone is immediately below the unconformable contact with the basal member of the overlying latest Eocene to earliest Oligocene Keasey Formation. The genus name is preoccupied by *Nehalemia* Blake, 1973, an asteroid echinoderm from the middle member of the Keasey Formation in Columbia County, Oregon. The type localities for both species are on the Nehalem River, approximately 25 km apart and with a vertical stratigraphic separation of approximately 450 m. Although the taxa are in separate phyla, the geographic and stratigraphic proximities of the type localities support the decision to avoid an orthographically similar replacement name.

Intaglicollonia is monotypic and its type species name retains the specific epithet originally proposed under *Nehalemia* by Hickman (1974). Although the genus is monotypic, it is the basal member of a putative evolutionary lineage in which intraspecific sculptural polymorphism has been studied, and named patterns of incised lines have an ontogenetic order of appearance in individuals (Noda and Ogasawara, 1976). Further study of variation in the onset of timing of the incised patterns has led to a model of heterochronic evolution in the lineage (Majima and Murata, 1992). The genus also has figured in the identification of the late Eocene origins of north Pacific deep-water communities (Hickman, 1984), in the characterization of biotic response to the Eocene-Oligocene climatic transition (Hickman, 2003), and in the reconstruction of patterns of trans-Pacific migration (Hickman, 2003; Amano, 2005).

Blake's (1973) genus is also monotypic and of considerable interest as a component of the famous Mist fauna in northwest Oregon in the upper part of the middle member of the Keasey Formation. The Mist locality is noteworthy as a Tertiary crinoid Lagerstätte (Moore and Vokes, 1953) as well as for its well-preserved asteroids, ophiuroids, and echinoids (Burns and Mooi, 2003). The carbonate layers at the Mist Locality are also noteworthy for providing petrographic and isotopic evidence of methanogenesis, possibly contemporaneous with the fauna and a potential cold seep environment (Burns et al., 2005).

New illustrations of the holotype of *Intaglicollonia hieroglyphica* are presented (Figures 1, 2) along with a detail of the fine engraved lines (Figure 3), which were interpreted originally as an unusual form of discordant (non-collabral) secretory activity by the mantle (Hickman, 1974). Discussion with Jonathan Todd (The Natural History Museum, London) raises the interesting possibility that the lines are "pseudoetchings" (*sensu* Palmer and Plewes, 1993; Todd and Palmer, 2002) generated as an active secretory response to the presence of a thin, tubular commensal cnidarian. In this instance the shallowly-incised lines would represent systematic and continuous growth response by the snail to deformation of the periostracal sheet at the growing shell margin. Similar active deformation responses have been reported in fossil bivalves (Todd, 1993).

Intaglicollonia, *Phanerolepida* Dall, 1907 and *Cantrainea* Jeffreys, 1883 are known only from deep-water faunas and sedimentary facies (>200 m) and are distinguished from the shallow-water "dwarf turbans" of the colloniine genus *Homalopoma* Carpenter, 1864 by their larger size and lack of nodulose spiral ribs separated by deep grooves. Shells of the Mediterranean type species, *Homalopoma sanguineum* (Linnaeus, 1758) are 6–7 mm in diameter and red or pink in color, in contrast to the unpigmented shells of the larger-shelled species in the deep-water genera.

The replacement name *Intaglicollonia* is chosen to call attention to the finely-incised (*intagliare*) markings on the shell surface as well as emphasizing the taxonomic position of the genus in Colloniidae Cossmann, 1916, a basal gastropod family group with a concentration of morphological diversity in the Cenozoic fossil record (Hickman and McLean, 1990). Publication of the replacement name is prerequisite to a forthcoming reinterpretation of the taxonomy, paleoecology, and unusual features that *Intagliocollonia* shares with fossil and living species of *Cantrainea* and *Phanerolepida*.

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LITERATURE CITED

Amano, K. 2005. Migration and adaptation of Late Cenozoic cold-water molluscs in the North Pacific. In: A.M.T. Elewa (ed.) Migration of Organisms. Springer, Berlin. pp. 128–150.

Figures 1–3. Holotype (USNM 647339) of *Intaglicollonia hieroglyphica* Hickman, 1979; height = 11 mm, diameter = 16 mm **1.** Apical and **2.** Abapertural view. **3.** Detail of incised sculpture on body whorl.

Blake, D.B. 1973. Ossicle morphology of some recent asteroids and description of some West American fossil asteroids. University of California Publications in Geological Sciences, 104: 1–59.

Burns, C. and R. Mooi. 2003. An overview of Eocene–Oligocene echinoderm faunas from the Pacific Northwest. In: D.R. Prothero, L.C. Ivany and E.A. Nesbitt (eds.) From Greenhouse to Icehouse: The Marine Eocene–Oligocene Transition. Columbia University Press, New York. pp. 88–106.

Burns, C., K.A. Campbell, and R. Mooi. 2005. Exceptional crinoid occurrences and associated carbonates of the Keasey Formation (Early Oligocene) at Mist, Oregon, USA. Palaegeography, Palaeoclimatology, Palaeoecology 227: 210–231.

Carpenter, P.P. 1864. Supplementary report on the present status of our knowledge with regard to the Mollusca of the West Coast of North America. Report of the 33rd Meeting of the British Association for the Advancement of Science (Newcastle-upon-Tyne), pp. 517–686.

Cossmann, M. 1916. ["1915"]. Essais de Paléoconchologie Comparée. Vol. 10. Paris: Privately published, 292 pp.

Dall, W.H. 1907. Descriptions of new species of shells, chiefly Buccinidae, from the dredgings of the U.S. "Albatross" during 1906, in the northwestern Pacific, Bering, and Japanese Sea. Smithsonian Miscellaneous Collections 50: 139–173.

Hickman, C.S. 1974. *Nehalemia hieroglyphica*, a new genus and species of archaeogastropod (Turbinidae: Homalopomatinae) from the Eocene of Oregon. The Veliger 17: 89–91.

Hickman, C.S. 2003. Evidence for abrupt Eocene-Oligocene molluscan faunal change in the Pacific northwest. In: D.R. Prothero, L.C. Ivany and E.A. Nesbitt (eds.) From Greenhouse to Icehouse: The Marine Eocene–Oligocene Transition. Columbia University Press, New York. pp. 71–87.

Hickman, C.S. and J.H. McLean. 1990. Systematic revision and suprageneric classification of trochacean gastropods. Natural History Museum of Los Angeles County Science Series 35: 1–169.

Jeffreys, J.G. 1883. On the Mollusca procured during the 'Lightning' and 'Porcupine' Expeditions, 1868–70. Part 6. Proceedings of the Zoological Society, London 1883, pp. 88–115.

Linnaeus, C. 1758. Systema Naturae per Regna tria Naturae 1. Regnum Animale. (10th Edition) Salvius, Stockholm, Sweden.

Majima, R. and A. Murata. 1992. Intraspeific variation and heterochrony of *Phanerolepida pseudotransenna* Ozaki (Gastropoda: Turbinidae) from the Pliocene Nobori Formation, Pacific side of southwestern Japan. Transactions of the Paleontological Society of Japan, N.S. 165: 1024–1039.

Moore, R.C. and H.E. Vokes. 1953. Lower Tertiary crinoids form northwestern Oregon. U.S. Geological Survey Professional Paper 233-E: 113–148.

Noda, H. and K. Ogasawara. 1976. On the variation of *Phanerolepida rehderi* MacNeil. Contributions from the Department of Geology and Mineralogy, Niigata University 4: 431–436. (in Japanese with English abstract)

Palmer, T.J. and C. Plewes. 1993. Borings and bioerosion in fossils. Geology Today 9: 138–142.

Todd, J.A. 1993. The bivalve shell as a preservation trap, as illustrated by the Late Jurassic gryphaeoid, *Deltoideum delta* (Smith). Scripta Geologica, Special Issue 2: 417–433.

Todd, J.A. and T.J. Palmer. 2002. Pattern versus process or informative versus ininformative Ichnotaxonomy: comments on Nielsen and Nielsen, 2001. Ichnos 9: 81–82.

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